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STUDIES IN CELLULAR SLIME MOULDS FROM INDIAN SOILS

I. On the Occurrence of *Dictyostelium mucoroides* Bref. and *Polysphondylium violaceum* Bref.

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(Communicated by Dr. S. N. Das Gupta, F.A.SC.)

INTRODUCTION

SEVERAL reviews have appeared on these simple but very interesting forms (Raper, 1941, 1951, 1956; Bonner, 1944, 1952; Sussman, 1955, 1956 *a*, *b*) and members of this group have been reported from different parts of the world. However, a review of the literature on Soil Microbiology showed an absolute lack of record of this group from Indian Soils, except that Raper in a personal communication informed Singh (1947) that he had isolated species of *Dictyostelium* from soils of Australia, India, Mexico, Brazil, Cuba and numerous stations throughout the United States. In view of the above fact and also because these organisms play a vital role in the food chain of the soil microbes, a detailed investigation of these was undertaken.

The present paper deals with two members of *Dictyosteliaceae* isolated from soils collected from areas round about Lucknow.

MATERIALS AND METHODS

The soil was collected from various areas round about Lucknow randomly selected from a depth of 6 inches using sterile spatula and paper bags. Every time the soil was collected in the morning and brought immediately to the laboratory for inoculations.

Hay-infusion agar (Raper, 1937, 1940, 1951) and Non-nutrient agar (Singh, 1946, 1947) were used for the isolation of these organisms from the soil.

In case of Hay-infusion agar a crumb of soil or soil-water suspension was placed directly on the agar surface having one-day growth of a suitable bacterium. The plates were incubated in dark at $22 \pm 1°$ C. Mature sorocarps were observed after a few days of incubation.

In case of Non-nutrient agar, a suitable bacterium growing on nutrient agar (2–7–day culture) was spread in the form of a disc, in the centre of which a crumb of soil or soil-water suspension was inoculated.

Non-nutrient agar (Singh, 1946, 1947) was found to be best suited for the study of the fruiting bodies of Acrasieæ. This medium which can be prepared very easily, excludes the possibility of a change in pH of the medium due to the fermentation of the substrate; it also excludes the possibility of a "competitive interaction between the bacterium and the Soil Acrasieæ" (Sussman, 1956 *a*) and being non-nutrient it does not support the growth of other unwanted organisms.

A pure culture was obtained by inoculating the spores of the slime mould at the intersection of two bacterial cross-streaks and then making sub-cultures from the ends of these streaks (Raper, 1951).

A rich growth of Acrasieæ was also observed in about two to three weeks' time in soil dilution plates poured for the study of soil fungi, using Brown's Synthetic Agar.

The isolation technique suggested by Kitzke (1952) was also tried with success.

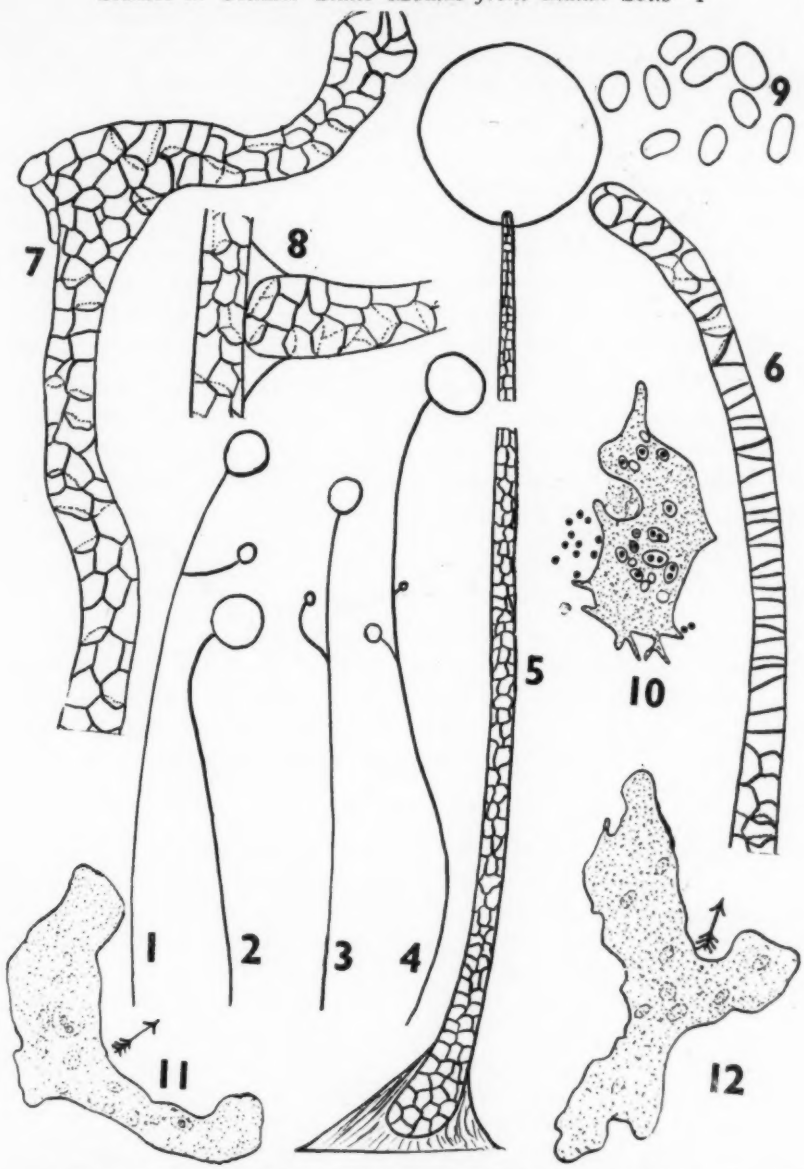
D. mucoroides could also be grown directly on sterilized Rabbit-dung balls inoculated with a suitable bacterium and placed in a humid chamber. Rabbit-dung balls have been used by Cohen (1953 *b*) also but in a different manner.

The two members of Acrasieæ, so far isolated, are maintained in this laboratory in "Pure-mixed" or "Two-membered cultures" with *Escherichia coli* or *Aerobactor aerogenes* on Hay-infusion and Non-nutrient agar. *E. coli* is long known to be a standard and most suitable food for these organisms.

OBSERVATIONS

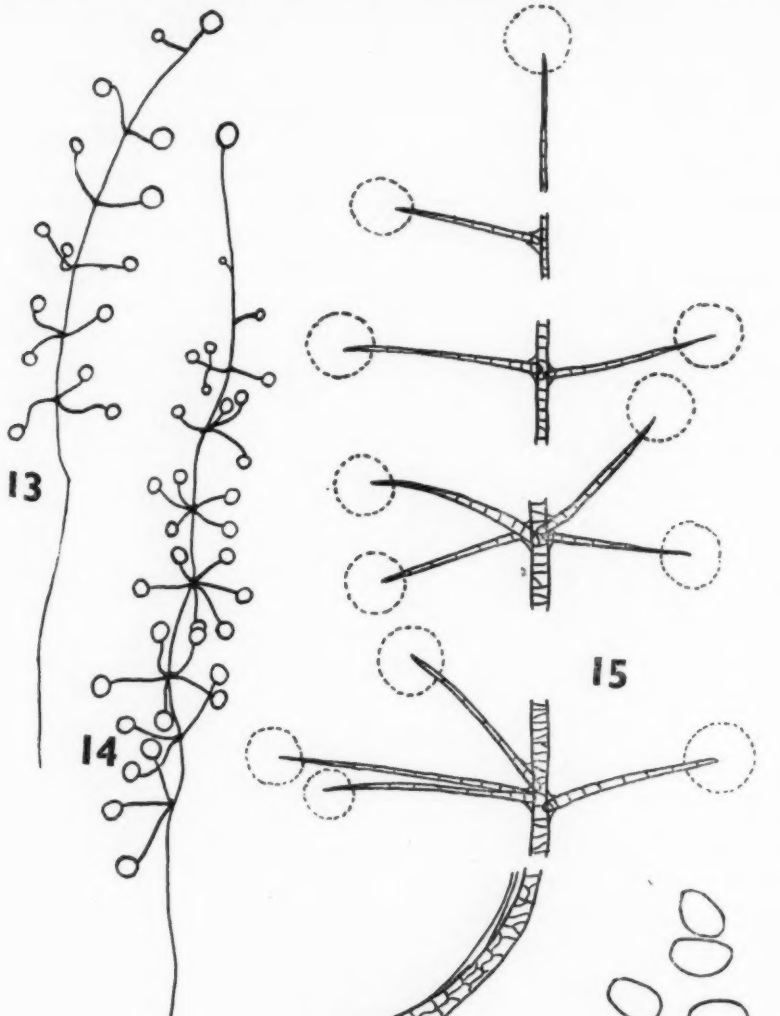
A study of soil samples from areas given in Table I has revealed the presence of *Dictyostelium mucoroides* Bref. and *Polysphondylium violaceum* Bref.

D. mucoroides (Text-Figs. 1–12) is characterised by milk-white sori 80–386 μ in diameter and borne on long, occasionally branched stalks, 0·6–3 mm. long and 12·8–16 μ wide in the middle. The sorocarps are solitary or gregarious. The stalk is composed of thin-walled cells. The full-grown myxamœbæ measure 14·4–19·2 $\mu \times$ 9·6–11·2 μ. The pseudoplasmodium is very variable in size. The spores are milk-white, oval to rod-shaped 4–7 $\mu \times$ 2·4–3·2 μ and are suspended in a droplet of slime. This species is very variable. Forms with short stalks resembling *D. brevicaule* Olive to forms with long trailing flexuous stalks resembling *D. giganteum* Singh have been observed in many of the soil isolates. Few of the sorocarps showed anomalous morphology.



TEXT-FIGS. 1–12. *Dictyostelium mucoroides* Bref. Figs. 1–4. Sorocarps, ×30. Fig. 5. An enlarged view of a sorocarp, ×150. Fig. 6. Terminal portion of the stalk, ×600. Fig. 7. Terminal portion of a stalk which had touched the agar surface and formed a pad of tissue at the point of contact, ×600. Fig. 8. Portion of the stalk with a branch, ×600. Fig. 9. Spores, ×1,280. Fig. 10. A myxamœba. *E. coli* cells are seen both inside and outside its body, ×2,500. Figs. 11, 12. Elongating myxamœbæ preparatory to aggregation. Arrows indicate the direction of the centre of aggregation, ×2,500.

P. violaceum (Text-Figs. 13–16) was identified by its light violet colour and by its " minute pine tree-like " (Harper, 1926) appearance. The soro-



TEXT-FIGS. 13–16. *Polysphondylium violaceum* Bref. Figs. 13, 14. Sorocarps, ×50. Fig. 15. An enlarged view of a sorocarp, ×300. Fig. 16. Spores, ×1,700.

carps are solitary or gregarious and consist of a stem, composed of a single row of cells except at the base and at a few other spots, bearing 2–10 whorls of branches, 80–100 μ long, each whorl 325–450 μ apart. The stem bears a terminal sorus 65–87 μ in diameter as do the other branches also and measures 3–4·5 mm. in length and 8–16 μ in width. The full-grown myxamœbæ measure 16–17·6 $\mu \times$ 4·8–12·8 μ. The pseudoplasmodium is very variable. The spores suspended in a droplet of slime, are oval to rod-shaped and measure 3·2–6·4 $\mu \times$ 1·6–3·2 μ. In cultures unbranched sorocarps resembling *Dictyostelium*, sorocarps with one branch and sorocarps with two opposite branches have been observed as described by Harper (1929).

In the present study (Table I) it has been possible to isolate *D. mucoroides* from 52 out of a total of 54 soil samples (pH 5·7–8·5) examined. This form has been isolated from dung composts, garden soil, forest soil, grassland soil, lake and river-side soils, cultivated soils and decaying wood and mushrooms. In contrast to the observations of Singh (1947) it has been isolated from soils under permanent grass also. A study of the rhizosphere of *Gomphrena globosa* also revealed the presence of *D. mucoroides*. This is in accordance with the observations of Sussman (1956 *a*).

P. violaceum could be isolated (Table I) only from 30 out of a total of 54 soil samples examined. It was present in soil samples of pH up to 7·1 but absent from those of pH 8·2–8·5. It was present in all the soil samples collected from Kukrail Reserve Forest, Residency and Sitapur Road. It is apparently absent from dung composts.

Discussion

The classical concept treated the Soil Acrasieæ as being coprifilic (Brefeld, 1869). But the isolation of *Dictyostelium mucoroides* from cultivated and uncultivated soils and *Polysphondylium violaceum* and *P. pallidium* Olive from the forest soils of Poland by Krzemienewski and Krzemienewski (1927) disproved this concept. Since then, they have been isolated from a variety of habitats by Raper and Thom (1932) and Raper (1951). In 1935, Raper (1935) established a new species (*D. discoideum*) isolated from decaying leaves from deciduous forest, North Carolina. Another new species (*D. minutum*) was described from leaf mould from deciduous forest, Virginia, Massachusetts and Maryland (Raper, 1941). In a study of the soils of Great Britain, Singh (1947) reported a new species, *D. giganteum*, isolated from an actively decomposing compost heap of straw and sludge, Rothamsted farm, Harpenden Herts, which has been treated as being a member of *D. mucoroides* complex by Raper (1951) and Sussman (1956 *a*). Singh (1947) also recorded the common occurrence of *D. mucoroides* in grassland and cultivated soils of

TABLE I

Locality	No. of soil samples examined	pH of the soil sample	No. of soil samples from which *D. mucoroides* was isolated	No. of soil samples from which *P. violaceum* was isolated
La Martineer College ..	6	5·7-6·7	6	4
Dilkusha Gardens ..	4	7·1–7·3	4	2
Kukrail Area:				
Kukrail Reserve Forest	4	6·4	4	4
Kukrail Village ..	16	8·2–8·5	16	..
Areas nearby Kukrail Bridge	8	6·0–7·1	8	6
Lucknow University Premises	6	6·5–6·8	6	4
Residency ..	4	6·7	4	4
Sitapur Road ..	6	5·8–6·0	4	6
Total ..	54	5·7–8·5	52	30

England, Wales and Scotland. Raper (1951) recorded *Dictyostelium* and *Polysphondylium* species in soil and leaf mould from Virginia, Illinois and Indiana. Mangenot (1952), in a study of the fungi attacking certain rooting timbers of France, recorded the presence of *D. minutum* on birch. Cohen (1953 *b*) isolated them from a forest floor in Georgia. The presence of *D. mucoroides* in the grassland soils of Laken Heath Warren was recorded by Warcup (1951). Farrow (1954) isolated *D. mucoroides* from the soils of Barro Colorado Isles, Rio Sardinella and Puerto Armuelles. Krzemieniewska and Badura (1954) in a study of the microflora of beech woods of Poland noticed the most common occurrence of *D. mucoroides* and *P. violaceum*. Raper (1956 *a*, *b*) described a new species *D. polycephalum* isolated from forest soils. Sussman (1956 *a*) reported species of *Dictyostelium* and *Polysphondylium* from various soil environs of the North-Western Campus, the Cook Country Forest Preserve and Winnetka Gold Course.

The occurrence of forms resembling *D. brevicaule* and *D. giganteum* lends support to the views of Raper (1951) and Sussman (1956 *a*) that they should be treated as members of *D. mucoroides* complex.

Few sorocarps of *D. mucoroides* showing anomalous morphology were comparable to the ones described by Raper (1939) for *D. discoideum*. Similar aberrant development of the fruiting bodies under sub-optimal conditions has been pointed out by Raper (1937, 1939), Singh (1947) and Cohen (1953 *a*).

As to the frequency of occurrence, Raper (1951) noticed the presence of at least one species of Acrasieæ in 37 out of 41 soil samples examined, *D. mucoroides* being isolated only from 22 soil samples. Cohen (1953 *b*) confirmed these relative frequencies. Sussman (1956 *a*) isolated members of *D. mucoroides* complex 24 times and *P. violaceum* 16 times out of a total of 52 soil samples examined. Our observations point out that the relative frequencies of the occurrence of *D. mucoroides* and *P. violaceum* is much higher in soils examined here.

The presence of *D. mucoroides* in soils of pH 8·5 is significant. These soils are extremely dry and support practically no vegetation except for a few scattered patches of grasses. It is likely that survival is by means of cysts which have been described in several members of this group (Cormier, 1955; Raper, 1956 *a*; Cormier and Raper, 1957). *P. violaceum* seems to be less adaptive to these conditions since it was not recorded in soils of pH above 7·2.

Summary

Two members of Acrasieæ, *Dictyostelium mucoroides* Bref. and *Polysphondylium violaceum* Bref. have been described for the first time from India. Certain facts of ecological interest have been pointed out and discussed. The results clearly indicate that the relative frequencies of the occurrence of these forms is much higher in soils examined here, as compared to previously published data.

Acknowledgement

The authors are thankful to Dr. B. N. Singh of Central Drug Research Institute, Lucknow, for providing the cultures of bacteria used in the present investigation and helping in the identification of the forms described, and to the authorities of the Council of Scientific and Industrial Research for the grant of a Fellowship to the junior author under the tenure of which this work has been carried out. Thanks are also due to Prof. S. N. Das Gupta for his critical suggestions and interest in the problem.

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ON THE ANATOMY OF TERATOLOGICAL SEEDLINGS—I

Cosmos bipinnatus Cav

By M. L. Banerji

(*Meerut College, Meerut*)

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(Communicated by Dr. V. Puri, F.A.SC.)

Literature on the anatomical study of abnormal seedlings is rather meagre. Guillaumin (1912) and Compton (1913) seem to have been the earliest workers. Holden and associates (1918, 1921, 1923), later Bexon (1920, 1925, 1926) and Bexon and Wood (1930) have been the only workers in the line who have carried out detailed investigations on abnormal seedlings. Malhotra (1935) investigated the anatomy of a tricotyledonary seedling of *Boerhaavia repens* and Cheenaveraiah (1949) described the anatomy of a tricotylous seedling of *Capsicum annuum*.

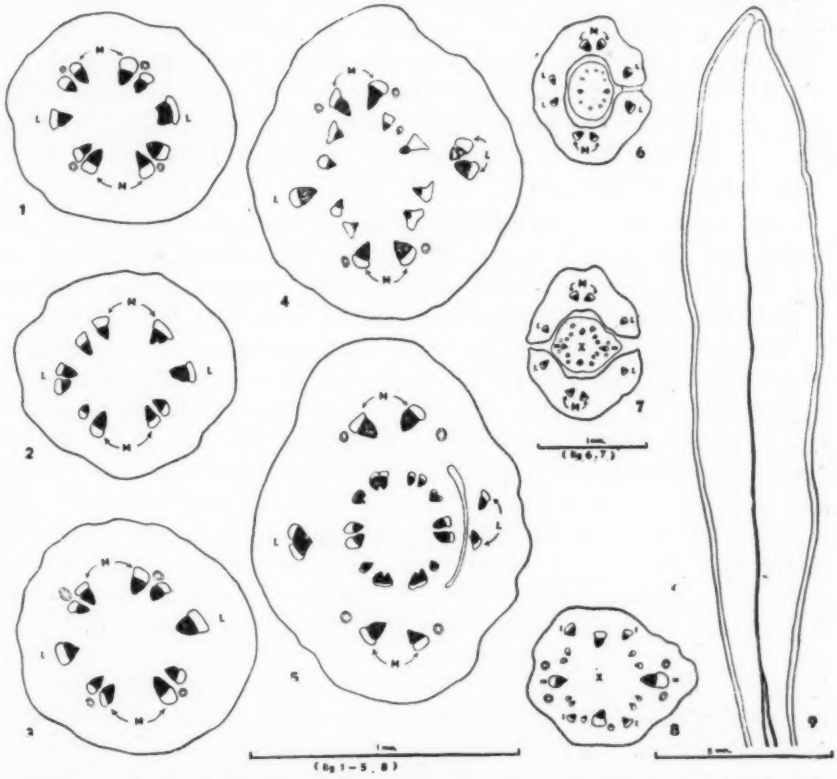
The discovery of a strain of *Cosmos bipinnatus* which produced a high percentage of abnormal seedlings has offered opportunity for a detailed study of the anatomy. The seedlings show deviations from the normal dicotylous condition in the direction of polycotyly (Banerji, 1956) and very rarely syncotylous modifications are also met with. Bexon and Wood (1930) came across seedlings of *Impatiens roylei* and *Sinapsis alba* wherein the deviation is also in the direction both of syncotyly and polycotyly.

Method.—Seedlings were uprooted at different stages of growth. They were preserved in F.A.A. Sections were cut at 14 μ thick and stained in crystal violet and erythrosin. The young seedlings did not take the stain well. Some cotyledons belonging to normal as well as to abnormal seedlings were cleared following the usual methods, and the venation has been studied.

Description

Normal seedling.—The root is tetrarch and in the region of transition four vascular bundles are formed after the xylem and phlœm bundles have undergone rotation. During the upward course the conjoint collateral bundles, that have been formed, increase in number. Two strands are separated out from the central bundles and these gradually occupy cortical positions. Each strand is single from the very beginning (Fig. 1); rarely as a

result of fusion of adjacent cauline strands a single bundle is formed (Fig. 2). The branches of these bundles are the future laterals of the cotyledons (Figs. 4 and 5). A pair of medians for each cotyledon is formed by the branches given off from adjacent bundles of the axis (Figs. 1, 2 and 3). These pairs of medians are at right angle to the laterals that have had their differentiation earlier (not in a morphogenetic sense). Higher up near the cotyledonary node, each lateral divides into two (Figs. 4 and 5) and each of the branches leads into a cotyledon. The medians of each pair come closer to one another (Fig. 6) during their upward course. In the meantime the cotyledonary tube gets separated from the axis by schizogenous splitting. The cotyledonary tube is very short and soon the two cotyledons get separated out as independent structures. In the axil of each cotyledon there is



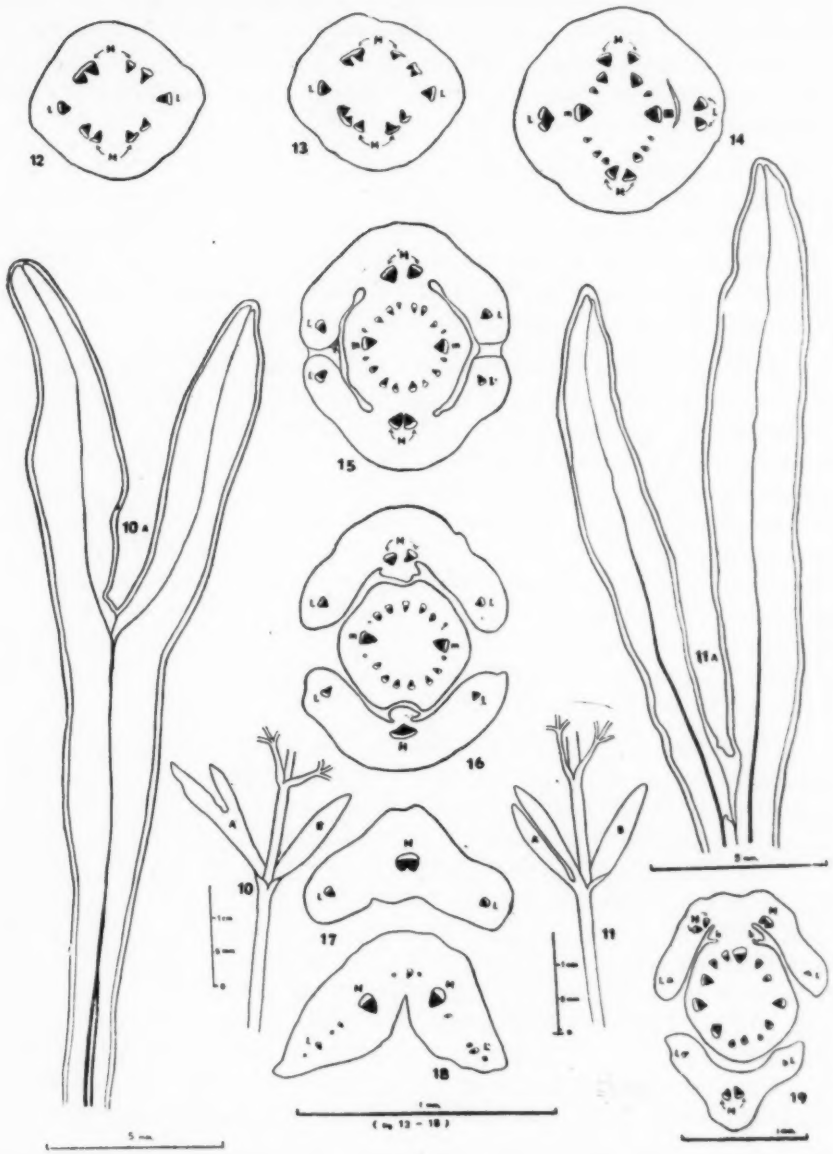
TEXT-FIGS. 1–9. Figs. 1–8. T.S. normal dicotylous specimen. Fig. 9. A normal cotyledon. *b.*, bud; *L.*, lateral of the cotyledon; *l.*, lateral of the foliage; *M.*, median of the cotyledon; *m.*, median of the foliage. (Xylem represented black.)

a bud. Each cotyledon has two medians running parallel to one another for 1/5 its length besides the two laterals (Fig. 7). Higher up, in the cotyledon, the two constituent medians come closer and finally fuse to form a single bundle which is continued up to the apex of the cotyledon (Fig. 9). Thus, there is a trilacunar condition, which is also reported by Sinnot (1914) for Compositæ.

In the foliage node, a single median is differentiated first (Fig. 6) and later are the two laterals (Figs. 7 and 8). The laterals for the two leaves are independent in origin and are not branches of a single bundle as in the cotyledons, neither are laterals at right angle to the median.

Hemitricotyls.—A large number of seedlings have been examined which showed different stages ranging from a mere notch at the apex of the abnormal cotyledon to those having the fission right up to the base (Figs. 10 and 11). Generally, in all cases, it was noticed that the two halves of the bifurcated cotyledon together have a surface area more than the surface area of the normal cotyledon. In rare cases, where the splitting was up to the base, each half of the abnormal cotyledon approximated the normal cotyledon in surface area.

The behaviour of the vascular strands of the hemitricotylous seedling is very interesting. The root is tetrarch like the normal seedling. In the hypocotyledonary region four vascular bundles are formed, and their number gradually increases. The laterals are differentiated first (Fig. 12) and get separated out of the vascular cylinder earlier, as it happens in a normal seedling. The paired medians for the cotyledons are separated later (Figs. 13 and 14); each lateral divides into two (Fig. 14) and thus far the sequence is exactly on the lines of a normal dicotylous seedling. The paired medians for the normal undivided cotyledon gradually pass into the cotyledon and after some distance fuse (Figs. 15 and 16). There is an axillary bud. The other cotyledon, which is lobed, also gets separated out of the cotyledonary sheath and has a bud in its axial too. The two medians leading to this abnormal cotyledon remain apart for some distance (Fig. 16), then fuse (Fig. 17) and again they separate out (Fig. 18). A small branch is given off near the point of bifurcation, and this later by further branching forms laterals. A little higher up, the tissues of the cotyledon divide and gradually two lobes of the cotyledon are formed (Fig. 10 A). The length along which the fused medians run determines the stage of lobing of the cotyledon. In specimens where the two lobes of the cotyledon are formed near the base, the distance of the fused part of the median is very short as compared to the cases where the lobing is near the middle or still higher up. This is in



TEXT-FIGS. 10–19. Figs. 10–11. Hemitricotylous specimens. Figs. 12–19. T.S. hemitricotylous specimen. *b.*, bud; *L.*, lateral of the cotyledon; *l.*, lateral of the foliage; *M.*, median of the cotyledon; *m.*, median of the foliage. (Xylem represented black.)

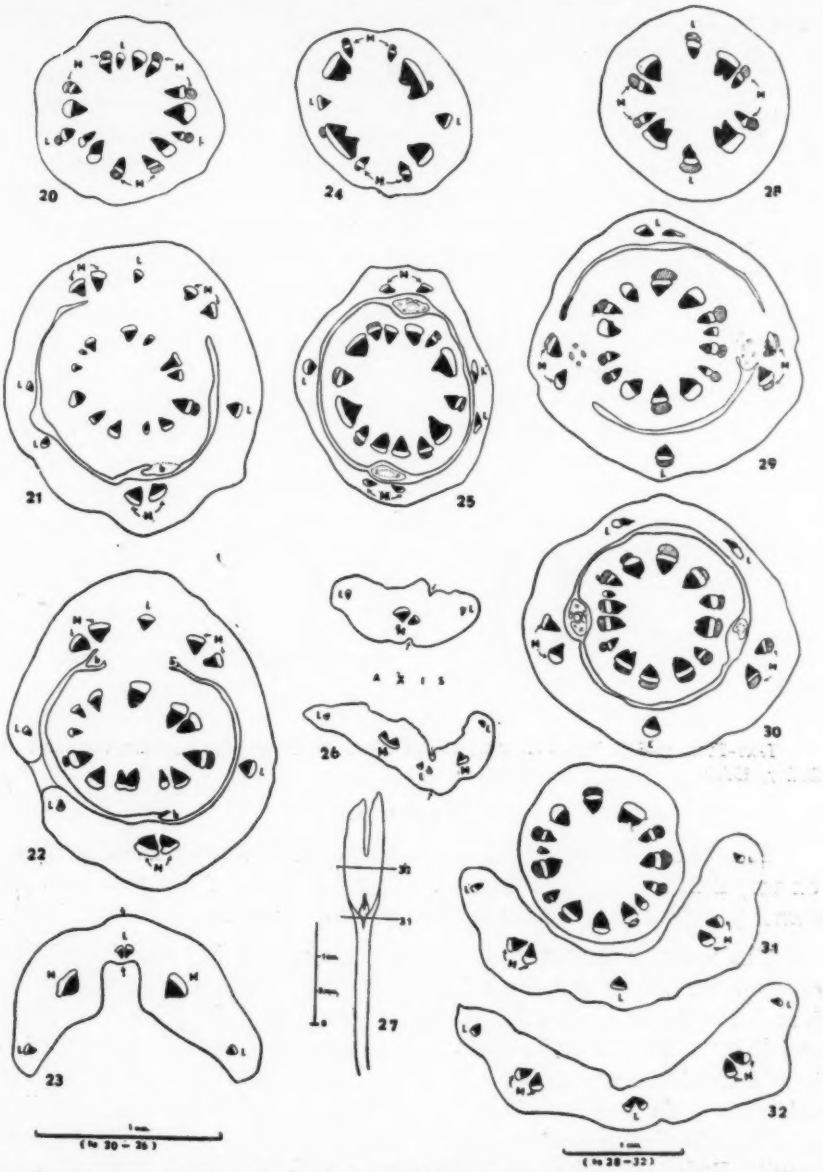
conformity with the observations of Holden and Bexon (1918) made on *Cheiranthus cheiri*. In some specimens, it has been observed, that the medians do not fuse but run parallel to one another for some length of the cotyledon, which is divided, and later one strand of the pair passes into each lobe of the cotyledon.

An interesting case of a hemitricotyl (Fig. 11) has been met with in which the differentiation of the laterals and the medians in the hypocotyledonary region follows the pattern of a tricotyl but one of the laterals loses its entity after a short distance, so that one of the cotyledons, which is lobed, has two pairs of medians (Fig. 19). There are two buds in the axil of this cotyledon; the buds are opposite to one another (Fig. 19 *b*).

Tricotyl.—In the hypocotyledonary region three laterals and three pairs of medians are differentiated (Fig. 20) although the root is tetrarch. The differentiation and departure of the laterals is earlier than the medians just as in the case of the normal seedlings. The three cotyledons are either equidistant or two are closer to one another. In all cases, one of the cotyledons gets separated out of the cotyledonary sheath earlier, and the other two separate out later (Figs. 21 and 22). Each cotyledon receives a paired median and two laterals (Figs. 21 and 22). The two medians of each cotyledon fuse at about 1/5 the length from the base, and the fused median now runs for the entire length of the cotyledon (Fig. 23), thus behaving as in the normal dicotylous seedling. It is significant to find a bud in the axil of each of the three cotyledons (Fig. 22 *b*).

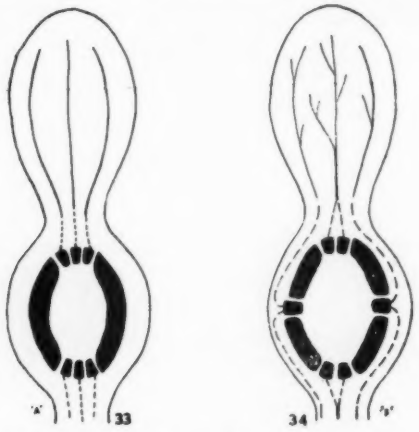
Hemitetracotyl.—The root is tetrarch. In the hypocotyledonary region the differentiation of the laterals and the medians follows the sequence and pattern of a normal dicotyledonous seedling, and like the normal or the hemitricotylous specimens, two sets of vascular strands are initially formed (Fig. 24). The two cotyledons get separated out from one another, and each receives a paired median and two laterals (Fig. 25). The two medians of each cotyledon do not fuse for about 1/3. the length of the cotyledon then they fuse and run for a short distance and separate out again; just as it happens in the abnormal cotyledon of a hemitricotylous specimen (Fig. 10 A). Each cotyledon gets divided (Fig. 26), with the result that a tetracotyl is formed. A branch is given off from one of the main branches of the median, and this branch by further branching forms the laterals of the lobes, just as in the case of the cleft cotyledon in a hemitricotyl.

Syncotyl.—A specimen was encountered which had a partly fused cotyledon (Fig. 27). Examination of the transections of this specimen showed that the origin of the laterals and the medians followed the plan of a normal



TEXT-FIGS. 20–32. Figs. 20–23. T.S. tricotylous specimen; Figs. 24–26. T.S. hemitetracotylous specimen; Figs. 27–32. T.S. syncotylous specimen; *b.*, bud; *L.*, lateral of the cotyledon; *M.*, median of the cotyledon (in Figs. 23 and 26 ↗ ↙ indicate the points of splitting of the cotyledon). (Xylem represented black, sclerenchyma hatched.)

seedling, *i.e.*, there are two laterals differentiated, followed by the differentiation of two medians (Fig. 28). There are two axillary buds developed (Fig. 29). The cotyledonary sheath splits along the side only (Figs. 30 and 31) so that an amphisyncotylous structure is formed. This has a lateral on either margin, two pairs of medians and in between the pairs of medians is one of the original lateral strand which has not divided (Fig. 32). About half the distance up the cotyledon the original undivided lateral strand divides (Fig. 32) and finally two lobes of the amphisyncotylous structure are also formed. These lobes are in reality with the two original cotyledons.



TEXT-FIGS. 33–34. Nodal anatomy of cotyledons in dicotyledonous seedlings (redrawn after Bailey, 1956).

DISCUSSION

It must be admitted in the very beginning that the present study is based on very little material as compared to the vast study of Bailey and his associates, yet the author makes bold to point out certain features of interest.

The vascular anatomy of angiosperm seedlings has been regarded as conservative (Foster and Gifford, 1958, p. 458). Bailey has emphasised that it is reasonable to assume that the unilacunar node is the primitive condition and that " trilacunar and multilacunar structures of angiosperms must have been derived at some evolutionary stage from a unilacunar condition. The trilacunar node may have been derived from a double leaf-trace condition or a single leaf-trace condition by the addition of a pair of lateral traces and gaps". Bailey (1956) has given the range of variability in cotyledonary nodal anatomy after a reconnaissance of seedlings belonging to 99 families of dicotyledons.

As has been mentioned previously, there is a double leaf trace along with two laterals going to each cotyledon of *Cosmos bipinnatus*. This condition is uniformly present in all the seedlings, be they normal or abnormal such as hemitricotyls, tricotyls, hemitetracotyls or even syncotyl. Thus, type 'F' which Bailey (1956, Fig. 34) found to be present in 10% of the seedlings investigated is exhibited by the seedlings of *Cosmos bipinnatus*, while type 'A' of Bailey (1956) (Fig. 33) is encountered in the foliage nodes of *Cosmos bipinnatus*. It is noteworthy to remember that a large proportion of the unilacunar angiospermous genera with double leaf trace are members of the order Ranales. The present observations also show that in the normal cases the two median traces approximate one another usually at about 1/5 the length upwards from the base and run up to the apex of the cotyledon, as has been recorded in *Amaranthus* and *Anchusa* (Marsden and Bailey, 1955, p. 45). Whenever the two central traces approximate and then diverge towards the apex of the cotyledon or the two traces remain independent throughout, there is the lobing of the cotyledon. And this results in either a hemitricotyl or a hemitetracotyl depending on whether one or both the cotyledons are effected. The condition of two medians running parallel remind one of the conditions present in *Clerodendron trichotomum*, Solanaceæ, and Labiatæ (Marsden and Bailey, 1955, p. 45).

It has been observed in the present study, that in the normal seedlings as well as in the abnormals, the laterals get differentiated first and get separated out of the vascular cylinder earlier than the medians. However this condition is reversed in the foliage leaf nodes.

From the present studies it can be concluded that hemitricotyly and hemitetracotyly are clear cases of splitting of one or both the cotyledons and this may be either by cotyledonary fission or by dichotomy of the growing point of the cotyledon as has been expressed by Holden and Bexon (1918). This is borne out by the fact that in a hemitricotyl or a hemitetracotyl only two sets of vascular strands are given off just as in a normal dicotylous specimen. Also, that there are only two buds in the axils of the cotyledons irrespective of the degree of lobing of one or both the cotyledons. The third possibility suggested by Holden and Bexon (1918) about the increase in cotyledonary number may be due to the downward displacement of one or more epicotyledonary leaves is not tenable because of the position and origin of the laterals and the medians.

To discuss the occurrence of tricotyledonary seedlings, it is necessary to review some of the previous work. Tricotyledons are known to occur in *Persoonia* (Proteaceæ) *Nuytsia* and *Loranthus* (Compton, 1913) and *Eugenia hookerii* (Johnston, 1936). Earle (1938) found embryos with three cotyledons

in *Magnolia grandiflora* as occasional abnormality, and Swamy (1949) found 87% tricotyledonous seedlings and 13% having four cotyledons in *Degeneria vitiensis*. This consistently tricotyledonous condition in *Degeneria* is a remarkable feature, and to find tricotyledonary seedlings in a highly advanced family like Compositæ is equally interesting. From the study of the anatomy, it is clear that the three cotyledons are independent structures not only externally but also internally. The plan of origin of the laterals and the medians is exactly like those in the normal dicotylous seedlings except for the increase in the number to three sets of vascular strands. This can also be substantiated by the presence of a bud in the axil of each of the three cotyledons. One specimen has been studied which had three sets of vascular strands in the hypocotyl but had only two cotyledons. In this case, one of the cotyledons is in fact a fused compound structure which has two pairs of medians and two laterals, as one of the original strands had not divided to form the laterals as has been noticed in the case of the syncotyl. Cheenaveraiah (1949) worked out the anatomy of a tricotylous seedling of *Capsicum annuum*, and concluded that the increase in number of cotyledons was a result of splitting but the figures that he has given show that all the three cotyledons are of independent origin.

From the study of abnormal seedlings of *Cosmos bipinnatus* it seems possible to assume that a tricotyledonary seedling is not the result of splitting of a cotyledon. It is of significance to find that the procambial strands in buds (Fig. 29), that are in the axils of the cotyledons, do not have any connection with the vascular bundles of the axis.

It is hoped that much more exhaustive and comprehensive accounts of abnormal seedling anatomy will be possible before long.

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ONTOGENETIC STUDIES IN *SARCANDRA IRVINGBAILEYI* SWAMY

I. The Structure of the Shoot Apex and Ontogeny of Leaf

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DURING the past twenty-five years, investigations over a variety of angiospermous shoot apices have brought in increasingly clear evidence in favour of Schmidt's (1924) tunica-corpus concept. According to this concept, the angiospermous shoot apex is composed of a central mass of cells called the *corpus*, covered over by one to several discrete surface layers of cells which collectively constitute the *tunica*. In 'tunica' the cells divide essentially in anticlinal planes and surface growth predominates. The 'corpus', on the other hand, is a homogeneous mass of cells. Division in these cells takes place in diverse planes thereby contributing to an increase in volume.

Detailed account of leaf histogenesis employing modern concepts and techniques was initiated by Foster (1936). These studies, which are exploratory in nature, enlighten the principles underlying the morphology of the leaf, cataphyll, phyllode and other appendicular structures. The present investigation concerns the structure of the shoot apex and the course of leaf initiation in a vesselless dicotyledon.

MATERIALS AND METHODS

The materials used in this study were collected in the forests of Peermade (Kottayam District, Kerala State) in the month of August 1957. During this period of the year, the plants are in active vegetative phase, although some of the fruits of the previous year are still undergoing the final stages of development. Vegetative buds and embryonic leaves were pickled in Craf and formo-acetic-alcohol. Customary methods of dehydration and embedding in paraffin wax were followed, and sections were cut at thicknesses varying between 8 and 10 μ and stained either in iron-alum-hæmatoxylin-erythrosin combination or tannic acid-ferric chloride schedule (Foster, 1934).

OBSERVATION

Structure of the shoot apex.—As has been detailed in the taxonomic description of the plant (Swamy, 1953), the phyllotaxy conforms to the opposite decussate pattern. The shoot apex is enclosed by the primordia or young leaves (one or two pairs) which in turn is surrounded by the vaginate cup formed of the fused petiolar bases of opposite leaves at the preceding node (Fig. 9).

Shoot apex: *Maximal stage.*—At the maximal stage of plastochron the shoot apex appears as a dome (Fig. 1). The number of tunica layers is generally two, although there is a tendency towards an increase up to four during this phase. The plane of division in the third and fourth layers is often periclinal. Because of the predominance of the two-layered tunica in all stages of development, the third and fourth layers are probably to be considered as a stratification of the corpus. The corpus exhibits more or less clearly marked zonations. The central mother cell zone is surrounded laterally by a radiating zone of cells and subjacently by the rib-meristem. The topographical relationships of the respective zones (Fig. 2) are as follows:

Tunica ——	Zone 1 ——	Two layers T-1 and T-2.
Corpus ——	Zone 2 ——	Central zone (mother cell zone).
	Zone 3 ——	Radiating zone, one on either side of the central zone as seen in median longitudinal section.
	Zone 4 ——	Rib-meristem at the subjacent level.

Certain cells of both tunica and corpus tend to stain differentially with nuclear and cytoplasmic stains. A group of cells situated towards the centre of the mother cell region at the distal end exhibits a relatively vacuolated cytoplasm and stains less deeply than the surrounding cells of the corpus in which the cytoplasm is less conspicuously vacuolate. Similarly, the cells of tunica that abut the vacuolated zone of corpus are also vacuolated and stain lighter (Fig. 1 and VR in Fig. 2). The same picture is presented in serial transverse sections of the shoot apex at the corresponding level. Although this differential vacuolation in the tunica and corpus is discernible more or less in all stages of plastochron, the phenomenon is more markedly seen at the maximal stage.

The rib-meristem is composed of vacuolated cells and its immediate derivatives possess smaller cell volume with readily staining protoplasts. These cells later enlarge to become the parenchymatous pith.

In the present investigation, the maximal stage of the shoot apex is taken to represent that particular phase wherein the cells in the flanks of the second tunica layer have undergone periclinal division to form the initials of the foliar primordium. Upon such consideration, the diameter of the apex (*i.e.*, the inter-leaf-primordial distance) at this stage measured in the median plane varies between 256 and 270 μ; the height measured from the base of the corpus to the apex of the dome is 88 μ.

Minimal stage.—As compared with the maximal stage, the apex at the minimal stage is very much reduced in size, *i.e.*, diameter 98 μ and height 42 μ. In shape, the apex is almost flat (Fig. 3). The number of tunica layers remains constantly two, although sometimes a third layer may also be present. The zonate pattern of corpus becomes less defined; so also the relative degree of vacuolation of the centrally situated cells of the tunica and the subjacent cells of the mother cell zone (Fig. 3).

In the duration between the maximal and minimal stages, the histological features present somewhat a transitional picture. The distinction between the tunica and corpus becomes less definable, partly owing to the onset of divisions in anticlinal planes in the third layer and partly due to the absence of a differential vacuolation amongst the cells of the apex (Fig. 4). The zonation pattern also appears variable consequent upon the portrayal of somewhat uniform histological features of the concerned cells of the corpus. The shape of the apex fluctuates within narrow limits from that of a slightly raised structure to a shallow dome-like structure (Fig. 4). The signs of stratification of the corpus cells become evident when the apex reorganises from the minimal to the maximal phase, *i.e.*, during the elongation of the internode.

The important structural features of the shoot apex during a plastochron may be summed up as follows:

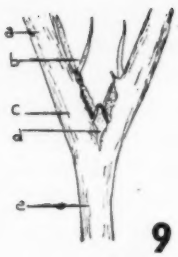
(1) Shoot apex exhibits larger area; differential vacuolation of the central region of the tunica and corpus is conspicuous; zonation of the corpus is at its height of definition; corpus exhibits stratification and outer two cell layers simulate the tunica layers—Maximal phase (Figs. 1 and 2).

(2) Shoot apex exhibits smaller dimensions; vacuolation of the central region of tunica and corpus becomes markedly less defined; stratification and zonation of the corpus are less evident; tunica is two-layered—Minimal phase (Fig. 3).

(3) Most of the above characters present intermediate condition during the resolution of the shoot apex from minimal to maximal phase. Stratification of the corpus becomes evident during these phases.

Ontogeny of the leaf: Apical growth.—During vegetative growth, leaf primordia arise in an opposite and decussate pattern on the stem apex, thus establishing the phyllotaxy of the adult plant. One or a pair of cells belonging to the second tunica layer (at times in the third stratified layer also) and lying toward the side of the meristematic dome divides periclinally. This division causes a slight protuberance at the corresponding areas on the apex (arrow in Fig. 6). These points of initiation represent the origin of the foliar buttresses. Simultaneously with this differentiation, some of the cells adjoining the base of the initiating cells of the primordia and belonging to the corpus divide in diverse planes, thereby heightening the primordium. The activity of the corpus derivatives ceases at a time when the sub-apical-initial cell becomes established in the primordium (Fig. 10). Thus, when the primordium attains an approximate height ranging from 70 to 95 μ (as measured from the distal extremity of the radiating zone to the tip of the primordium) the sub-apical-initial cell becomes manifest. With these changes taking place during the plastochron, the distinctiveness of the second tunica layer becomes somewhat less obvious and it becomes impossible to identify this layer in the leaf primordium proper. The cutting off of derivatives from the sub-apical-initial cell, which results in the vertical extension of the primordium also causes a discontinuity of the second tunica layer (Fig. 12).

The early divisions in the sub-apical-initial cell are periclinal (Fig. 11). But soon, for a time, divisions in anticlinal plane also become fairly frequent. It may be particularly noted that it is during this phase that the leaf primordium attains considerable dimension in girth. Thus, the onset of anticlinal division in the sub-apical-initial cell coincides with the increase in dimension of the primordium until it attains a height of 90–120μ. When the sub-apical-initial cell undergoes a division in anticlinal plane, the daughter cells tend to present more or less similar histological characteristics—cell dimensions, cytonuclear ratio, degree of vacuolation of cytoplasm, etc. Thus, it is quite possible that such a stage is liable to be misinterpreted as representing the presence of more than one functional sub-apical-initial cell. The similarity between the daughter cells is sometimes more enhanced particularly when both the cells are in a state of division (Fig. 15). At other times, a group of four (Fig. 14) or six cells (Fig. 13) present somewhat identical appearance. In the latter case, the interpretation of such a stage, in all likelihood, would be to consider the central cells of the two tiers to be sub-apical-initial cells (after a periclinal division), and the cells of the tiers on either side as derivatives of the sub-apical-initial cell through anticlinal walls during the previous cell generations, which in turn would have undergone division in periclinal plane during the preceding cell generation. In later stages, division in the



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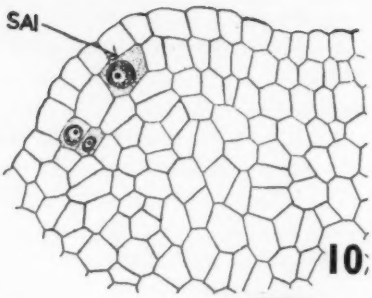

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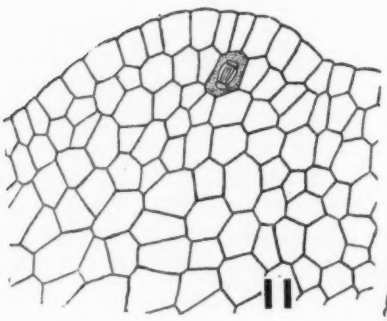

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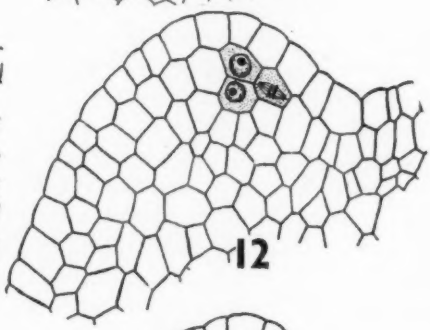

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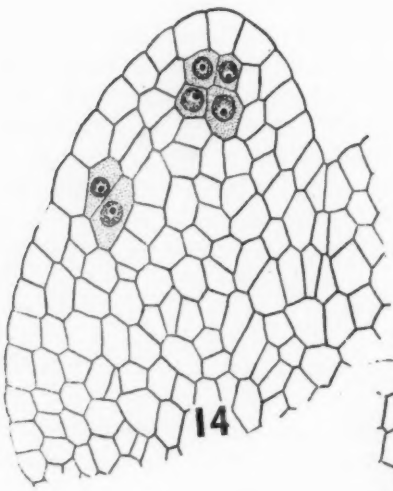

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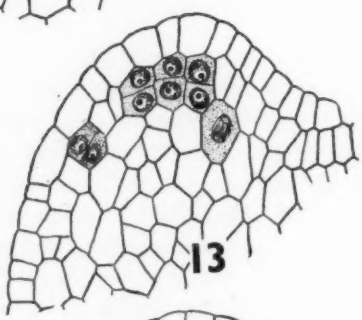

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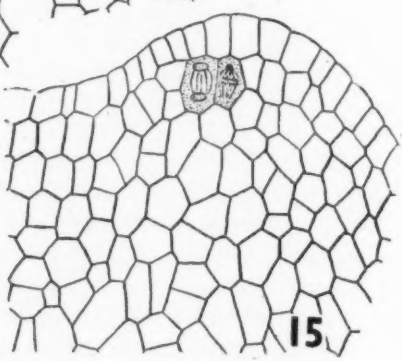

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FIGS. 9–15

sub-apical-initial cell is predominantly in the periclinal plane (Fig. 5), the divisions in the anticlinal plane being very infrequent.

Procambialization of the primordium is initiated when it measures about 170 μ in height. The differentiation of this tissue is progressive and acropetal. Two procambial strands in continuation of two independent vascular bundles of the subjacent region differentiate acropetally into the base of the primordium. The two strands (which represent the vasculature of the laminal-midrib) remain distinct and continue to differentiate as such in the median part of the leaf until the sub-apical-initial cell ceases its activity. The activity of the sub-apical-initial cell continues until the primordium attains a height of 520 μ.

Marginal growth.—Marginal growth is generally observed to occur in primordia of about 490 μ high. The petiolar-midrib portion is differentiated early during the apical growth of the leaf primordium as stated in the previous paragraph. The lamina develops subsequently by the activity of the marginal meristem. At the time of formation of the sub-marginal-initial cell, the primordium as seen in transection, presents a somewhat heart-shaped outline (Fig. 16). If the leaf primordium is viewed three-dimensionally the first tunica layer of the shoot apex continues over the leaf primordium as its epidermis. The sub-marginal-initial cell takes its origin in the hypodermal layer and is located on the elevated flanks on either side of the adaxial depression of the primordium. The initials are relatively more conspicuous by their slightly enlarged size and more pronounced polygonal outline (Fig. 16). The epidermal cell that abuts the sub-marginal-initial cell functions as the marginal-initial cell and it undergoes repeated divisions essentially in anticlinal planes (Figs. 17 and 18), thereby contributing derivatives that constitute the adaxial and abaxial protoderms, which perpetuate as the upper and lower epidermis of the leaf respectively. In the course of the present investigation no evidence could be gathered to show that marginal-initial cell or its derivatives ever divided in periclinal planes. The sub-marginal-initial cell behaves differently from the marginal-initial cell in that its derivatives contribute to the entire mesophyll tissue.

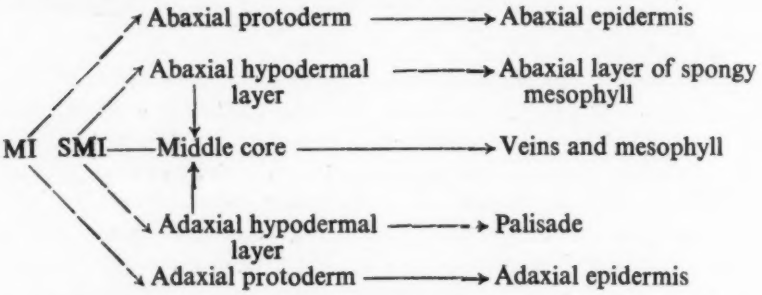
The activity of the sub-marginal-initial cell may be described under two heads, namely, early marginal growth and late marginal growth as follows:

Early marginal growth.—During early marginal growth, the sub-marginal-initial cell divides anticlinally contributing cells to the abaxial and adaxial hypodermis (Fig. 16). Through periclinal division (Fig. 16) the sub-marginal-initial cell contributes derivatives to the central core. The

cells of the abaxial and adaxial hypodermis often divide anticlinally and periclinally or obliquely (Figs. 16 and 17) and contribute derivatives to the cortical regions of the midrib.

Late marginal growth.—It is during this phase that the laminal differentiation takes place. The activity of the sub-marginal-initial cell is now somewhat different from that of the early marginal growth described above.

The entire internal tissue organisation of the leaf—the palisade, the spongy parenchyma, the veins, etc.—owe their origin to the sub-marginal-initial cell either directly or indirectly, as follows:



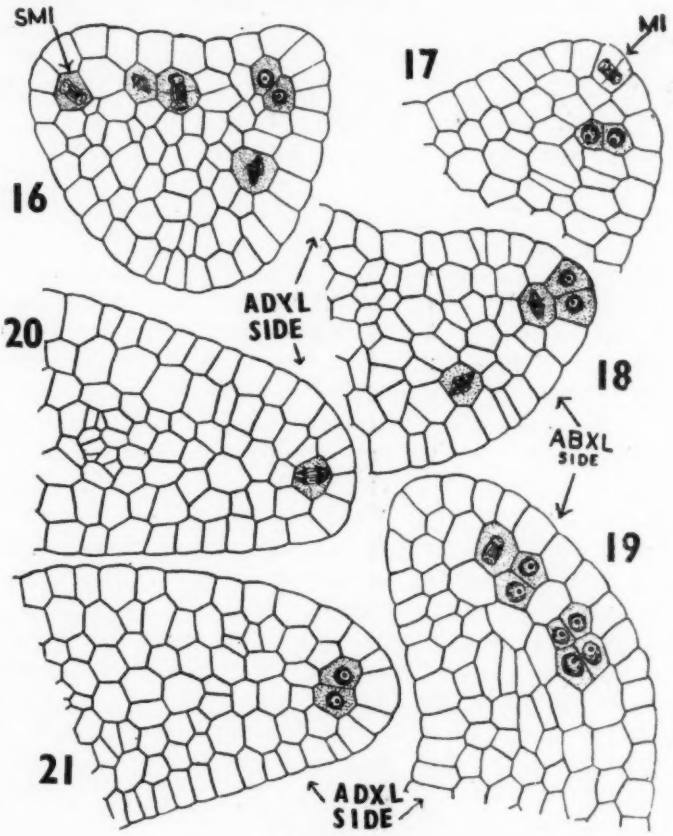
MI, Marginal-initial cell; SMI, Sub-marginal-initial cell.

The sub-marginal-initial cell (hereafter designated as *Smi* cell) divides periclinally contributing cells to the central core (Fig. 20) and anticlinally (Fig. 18) giving derivatives to the abaxial and adaxial hypodermal layers. The derivative cells in turn divide anticlinally (Figs. 8 and 18) thus perpetuating themselves. It should be noted that frequently the abaxial and adaxial layers of cells also divide periclinally (Figs. 7, 8 and 19) contributing cells to the central core. Thus, the 'central core' in this case should be taken to denote the cell layers that extend between the abaxial and adaxial hypodermal layers. On the whole, it was noticed that the periclinal division in the abaxial hypodermal layer occurs at more frequent intervals than in the adaxial hypodermal layer. Thus, the contribution of the abaxial hypodermal layer to the constitution of the central core is relatively more and on a larger scale than that by the adaxial hypodermal layer. This phenomenon results in a slight incurling of the lamina in the early stages.

Often, two cells placed adjacently were noticed to occur (Fig. 21) instead of the usual single *Smi* cell. Under such circumstances both the cells function in a like manner.

The derivatives of the *Smi* cell to the adaxial side align into a relatively undisturbed regular row (Figs. 7 and 8). These cells which are homologous

with the palisade cells lack the conventional form in being more or less cubical or less pronouncedly rectangular. In transections of younger leaves a majority of these cells exhibit infiltration or inclusions or deposits that stain brilliant reddish with safranin or hæmatoxylin. At least, in part, these inclusions appear to be phenolic compounds.



FIGS. 16–21

DISCUSSION

In general, the structure and behaviour of the shoot apex of *Sarcandra irvingbaileyi* shows marked similarities with those of the other vesselless dicotyledonous representatives that have been investigated (Gifford, 1950). The normal number of tunica layers in *Sarcandra irvingbaileyi* is two; sometimes the outermost layer of the corpus presents similarities to the

tunica layers, whereby during such phases there appears to be a total of three (or occasionally four) layers of tunica. These additional layers resemble tunica not only in the morphological appearance but also in their behaviour; that is, the constituent cells divide more frequently in anticlinal planes, and soon after a series of such divisions, the newly formed cells align themselves in such a way as to simulate the outer tunica layers. This state of affairs has been reported in other vesselless dicotyledonous genera. In *Drimys winteri* and *Drimys lanceolata* (Winteraceæ), the normal number of tunica layers is two, increasing to three occasionally; in *Trochodendron aralioides* (Trochodendraceæ), normally two, sometimes at least three; in *Tetracentron sinense* (Tetracentraceæ), one or two, in the latter case the inner layer is rather weakly established. In *Pseudowintera axillaris* var. *colorata* (Winteraceæ), however, there appears to be a stable number of two tunica layers (Gifford, 1950). It may be remarked that Gifford's investigation of the shoot apex of *Pseudowintera* has not been as detailed as of *Drimys*. May be, more detailed investigation on this plant may also display a variation in the number of tunica layers. Furthermore, there are reports regarding the stratification of the corpus cells in vessel-bearing dicotyledonous plants also. The extensive work of Schnabel (1941) in *Silene maritima* is worthy of note in this connection. Of the one hundred and twenty-eight shoot apices studied by the above author, a four-layered tunica occurs in 40·6%, a three-layered tunica in 55·6% and found periclinal divisions in T-3 to the extent of 2·4% and T-4, 1·5%. On the basis of this evidence, he concluded that the plant possesses a three-layered tunica definitely and that the fourth layer is the stratification of the corpus cells. In *Hypericum uralum*, Zimmermann (1928) came to the conclusion that the tunica layers do not fluctuate in a leading shoot but that the upper cells of the corpus form a definite layer at the maximal stage of a plastochron. The researches of Cross and Johnson (1941) in *Vinca rosea* show that the upper layer of corpus maintains a tunica-like alignment until after leaf formation. Stratification of corpus cells is also seen in the shoot apex of *Polyalthia longifolia* (Ramji, 1960). A study of Gifford's review (1954) clearly emphasises a two-layered tunica as the norm and variation lies on the neighbourhood of this number. This is true in the vesselless dicotyledons also and in this respect the latter group of plants do not deviate from the vessel-bearing dicotyledons.

The question arises whether these outermost layer or layers of corpus should also be considered as belonging to tunica. It must be pointed out that the tunica-like behaviour of the corpus cells is only occasional; in other words, such a behaviour is confined mostly to the maximal phase of a plastochron. On the other hand, the tunica layers (in the strict sense)

do not deviate from their normal behaviour. Therefore, it may not be very correct to categorise such cell layers under tunica. In Gifford's (1954) opinion the accessory 'tunica' layers (originating in the corpus) are to be looked upon as a stratification of the corpus. It is quite probable that superficial cells of the corpus, at one phase of the ontogeny of the shoot apex, undergo a large number of divisions by anticlinal walls. This phase generally coincides with the increase in the dimensions of the shoot apex, *i.e.*, the attainment of the maximal phase. During such a dynamic phase, the simulation of a few layers of corpus cells to tunica may, in reality, be looked upon as a necessary prelude towards the attainment of an increase in the overall size of the shoot apex. Therefore, the concerned cells of the corpus should, at one time or other, undergo successive anticlinal divisions in order to keep pace with the increase in surface area of the tunica and, in turn, of the shoot apex as a whole.

The available data on the dimensions of the shoot apex of vesselless dicotyledonous genera are as follows (those with asterisk taken from Gifford, 1950):

Species	Dimensions		
	Maximum width	Minimum width	Height
*Drimys winteri** and *Drimys lanceolata**	98–130 μ	57–70 μ	..
*Pseudowintera axillaris** ..	147–154 μ	Nil	32 μ
*Trochodendron aralioides** ..	229–240 μ	Nil	65 μ
Sarcandra irvingbaileyi ..	256–270 μ	98 μ	88 μ

It will be seen from the above table that the shoot apex of *Sarcandra* presents the largest dimensional values as compared with the other vesselless dicotyledonous plants, its nearest size being exhibited by *Trochodendron aralioides*.

That the shoot apex of angiosperms exhibits changes in shape during different stages of development is well known. Of the vesselless dicotyledons, the shape in the two species of *Drimys* studied by Gifford (1950) ranges from flat to concave; in *Pseudowintera axillaris* it is slightly convex at the maximal phase; in *Trochodendron aralioides* it is dome-shaped at maximal phase. The range of variability in *Sarcandra* is from that of a

dome (maximal stage) to a flat one (minimal stage). Thus, the maximal stage of plastochron in *Sarcandra irvingbaileyi* is more comparable with that of *Trochodendron* than with that of *Drimys*.

The shoot apices of angiosperms generally exhibit a zonate pattern in varying degrees and relative proportions. The zonation in *Sarcandra irvingbaileyi* is a feature that is well expressed at the maximal stage of plastochron. Particular mention may be made of the existense of a core of conspicuously vacuolated cells in the median part of the shoot apex. The occurrence of such a zone has also been reported in the other vesselless genera—*Drimys*, *Trochodendron* and *Tetracentron* (Gifford, 1950) and in a few species of vessel-bearing dicotyledons (Boke, 1941, 1951; Esau, 1942; Girolami, 1954; Reeve, 1942, etc.). Although its presence in vesselless genera appears to be quite uniform, any endeavour towards attaching phylogenetic significance to the phenomenon appears to be extremely remote in view of its occurrence also in families like the Cactaceæ (Boke, 1941, 1951), Linaceæ (Esau, 1942; Girolami, 1954) and Garryaceæ (Reeve, 1942).

Foliar ontogeny.—In *Sarcandra*, as in many other dicotyledons, the periclinal division occurs in the second tunica layer augmenting the formation of the foliar buttress. This course of leaf initiation seems to be a common feature to many dicotyledons and takes place irrespective of the number of tunica layers that are present in the apex. In cases where more than two tunica layers are shown, the participation of other layers varied in their contribution to the formation of the leaf primordium (Cross, 1937 *a*, *b*; Gifford, 1951; Reeve, 1942 and others). In *Sarcandra irvingbaileyi* the establishment of the sub-apical-initial cell is delayed until the primordium is 70 μ high and the corpus contributes towards the early apical extension of the primordium. The corpus derivatives continue to add cells to raise the primordium until the primordium is about 90 μ high. Such contribution of the corpus cells to the primordium proceeds for a time, hand in hand with the activity of the sub-apical-initial cell. In *Drimys winteri* var. *chilensis* also, a similar phenomenon has been reported (Gifford, 1951).

Variations occur in the early apical extension of the foliar primordium in a few vessel-bearing plants. Cross (1937 *a*) doubtfully expresses the opinion that corpus is not directly involved in the origin and extension of the foliar primordium in *Viburnum rufidulum* even though the establishment of the sub-apical-initial cell is delayed until the primordium is 170 μ high; the heightening takes place essentially due to intercalary growth. In contrast, the early establishment of the sub-apical-initial cell in the primordium of *Linum* (Girolami, 1954) restricts the contribution of the corpus deriva-

tives towards the early growth of the primordium. A similar condition as above has been observed in *Polyalthia longifolia* (Ramji, 1960). Further, Boke (1949) reports the presence of sub-apical-initial cell in *Acacia* as soon as a primordium is initiated.

There are reports regarding the possible presence of a group of sub-apical-initial cells during the apical extension of the foliar primordium or cataphyll or a phyllode. In the vesselless dicotyledon *Drimys winteri* var. *chilensis* (Gifford, 1950), a group of six sub-apical cells as promoting the apical growth of the leaf primordium has been reported. Gifford is of the opinion that "the group of six sub-apical cells (arranged in two tiers) has been formed from one 'mother cell.' One of the derivatives (probably the upper middle cell) would have enlarged and occupied momentarily a key position in anticipation of the next series of divisions". In *Sarcandra* also, a similar condition closely allied to *Drimys* is noticed. A group of four or six cells present somewhat identical appearance in contrast to the other cells. A superficial examination may lead one to suspect that all the cells of the group individually behave in the manner of sub-apical-initial cells. However, critical examination of successive developmental stages in *Sarcandra* indicates clearly that the cells of the complex are no doubt derivatives of the sub-apical-initial cell. But the complex, in relatity, represents a *stage* in differentiation. Thus, for example, when a sub-apical-initial cell undergoes successive divisions in the vertical plane so as to give rise to three cells and these cells in turn divide in transverse plane and when the time interval between the divisions is somewhat overlapping, it is no wonder that the result would be a group of six cells all of which look alike. Records of functioning of a group of sub-apical-initial cells are not wanting in the literature. Foster (1935) in *Carya* reports that a group of sub-apical-initial cells is evident, and this group is responsible for the heightening of the cataphyll primordium. Similarly, Boke (1949) attributes the apical growth of the phyllode primordium in *Acacia* to a group of sub-apical-initial cells. In *Sarcandra irvingbaileyi* there is no decisive proof to demonstrate the presence of a group of sub-apical-initials; because the multicelled appearance of sub-apical-initial complex in this plant does not characterise all stages during the extension of the leaf primordium. On the contrary, the multicelled condition occurs only during very early stages in the heightening of the primordium and that too, once in a way. Its presence is only apparent and not real.

In the observation part of the present paper it has been shown that during marginal growth in *Sarcandra*, the *Smi* cell divides anticlinally cutting off cells to abaxial and adaxial hypodermal layers. It divides periclinally

also and thus adds cells to the central core. The abaxial and adaxial hypodermal layers divide obliquely or periclinally and contribute derivatives to the central core. Even though both the abaxial and adaxial hypodermal layers contribute to the central core, the contribution of the adaxial side is far less than that of the abaxial side. In *Drimys*, Gifford (1951) has observed that the adaxial hypodermal layer, derived from sub-marginal-initial cell, generally divides in anticlinal planes. But often due to periclinal divisions, it yields derivatives to the central core. The outer cells resulting from periclinal divisions of the adaxial layer align into the first palisade layer, the next two inner palisade layers being derived from the middle core of cells. Thus, the origin of the middle core of cells in *Sarcandra* and *Drimys* follows similar pattern in being derived from the *Smi* cell, abaxial and adaxial hypodermal layers. But the amount of contribution of cells to the central core due to the activity of adaxial side is more pronounced in *Drimys* than in *Sarcandra*. Similar cases are seen in *Zea* (Mericle, 1950) and *Polyalthia longifolia* (Ramji, 1960).

The growth of the lamina in *Sarcandra* is accomplished through the activity of a single sub-marginal-initial cell as seen in a transection; sometimes, however, two adjacent cells occupy the locus. In the latter case, both the cells contribute towards the breadthwise extension of the lamina. Similar observation is reported by Gifford (1951) in *Drimys*. In this plant, there are as many as four cell rows of palisade tissue on the adaxial part of the lamina. Of these, the adaxial hypodermal layer matures into the palisade in which the cells are more or less isodiametric while the remaining three rows are constituted of relatively elongated cells. In *Sarcandra*, it is the adaxial hypodermal layer that matures into the palisade in which the cells do not conform to the conventional shape. In other words, a palisade layer in *Sarcandra* is ill-defined.

SUMMARY

This study concerns the structure and behaviour of shoot apex, initiation and growth of the leaf in a vesselless dicotyledon *Sarcandra irvingbaileyi* Swamy. During the maximal phase of plastochron, the shape of the apex is a dome with two definite tunica layers and additional stratified layers. Pronounced vacuolation with clear stratification of the corpus cells is characteristic of this phase. During the minimal phase, the shape of the apex is almost flat. Tunica layers are two in number. Vacuolation and stratification of the corpus cells are less pronounced.

The range of variability in the tunica layers of dicotyledonous shoot apices is briefly reviewed. As to the opinion in regard to the morphological

nature of the third (and sometimes fourth) accessory 'tunica' layers, it a suggested that these layers in *Sarcandra* is more akin to corpus than to tunica; the anomalous behaviour of these layers could be a mechanism towards the maintenance of constancy between surface growth of tunica and volume growth of corpus.

Initiation of the leaf takes place in the second tunica layer. Initial heightening of the foliar primordium is accomplished by the activity of the corpus. The sub-apical-initial cell in the leaf primordium is established when it is 70–80 μ high and stops functioning when the primordium is 520 μ high. While the apical growth of the leaf primordium is accomplished chiefly due to the presence of a single sub-apical-initial cell, sometimes a group of initial cells appears to be involved. In *Sarcandra*, the multicellular nature of the sub-apical cell complex represents only a stage in development.

The lamina is produced by the activity of the marginal meristem. The activity of the sub-marginal-initial cell (sometimes two) produces the inner tissues of the leaf. Certain developmental deviations during the formation of the central core of cells in the lamina are noticed, the most important one in *Sarcandra* being the contribution of the adaxial hypodermal layer to the central core.

Acknowledgement

My thanks are due to Professor B. G. L. Swamy for guidance and criticisms.

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EXPLANATION OF PLATES

PLATE I, FIGS. 1–2

FIG. 1. Median longitudinal section of the shoot apex at the maximal stage of plastochron showing the tunica-corpus alignment, × 600.

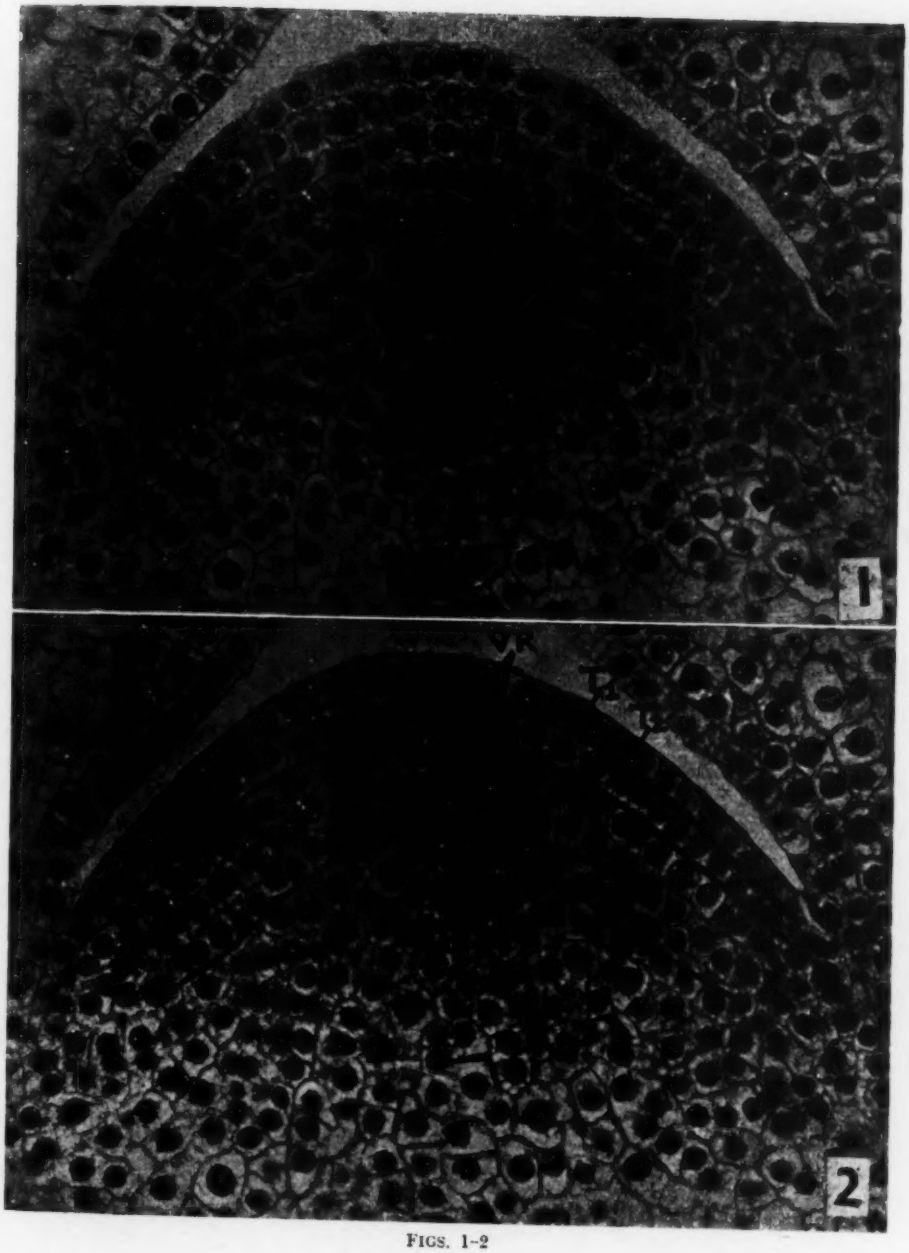
FIG. 2. Same as above with various zones Marked out, × 600. T-1, First layer of tunica. T-2, Second layer of tunica. Zone 2, Central mother cell zone of corpus. Zone 3, Radiating zone of corpus. Zone 4, Rib-meristem. VR, Vacuolated region restricted to tunica and corpus. Further explanation in the text.

PLATE II, FIGS. 3–8

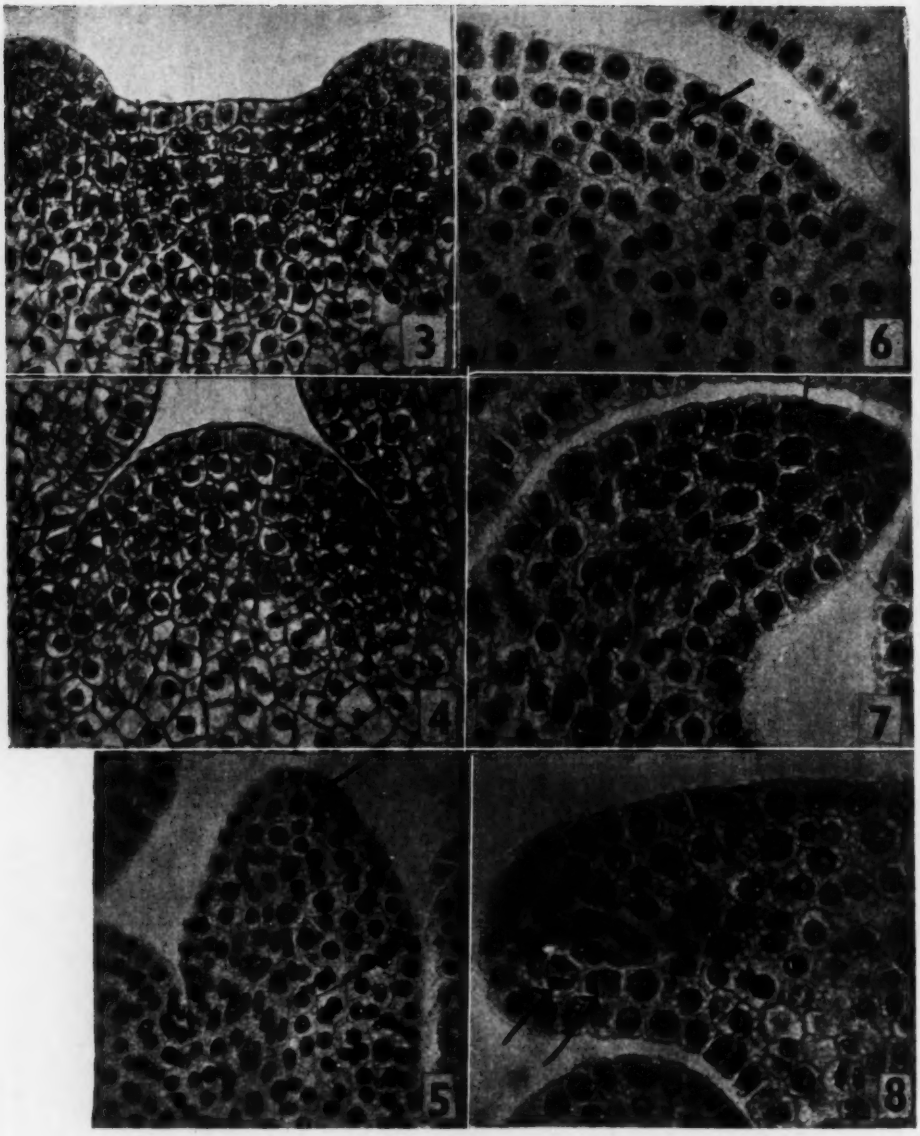
FIG. 3. Median longitudinal section of the shoot apex at the minimal stage of plastochron. Note the flat nature of the apex, × 330.

FIG. 4. A resolving shoot apex in median longitudinal section. Layering of the corpus cells is becoming evident, × 350.

FIG. 5. Median longitudinal section of a foliar primordium. Arrow indicates the periclinal division in the sub-apical-initial cell, × 350.



FIGS. 1–2



FIGS. 3–8

FIG. 6. Longitudinal section of the shoot apex showing the occurrence of periclinal division in the second tunica layer (indicated by arrow) and the formation of the foliar buttress, × 350.

FIG. 7. Transverse section of an embryonic lamina showing the occurrence of periclinal division in the abaxial hypodermal layer (indicated by arrow), × 400.

FIG. 8. Transverse section of an embryonic lamina showing the division of two adjacent cells of the adaxial hypodermal layer. One cell is dividing anticlinally while the other is dividing periclinally (indicated by arrows), × 400.

EXPLANATION OF TEXT-FIGURES

FIGS. 9–15. Fig. 9. Diagrammatic representation of the position of the apical bud. *a*–petiole; *b*–stipule; *c*–base of the petiole split open to show the apical bud; *d*–abaxial view of a developing leaf primordium; *e*–stem. Fig. 10. Longitudinal section of a foliar primordium showing the establishment of the sub-apical-initial cell. SAI–sub-apical-initial cell. Fig. 11. L. S. of a foliar primordium indicating the periclinal division in the sub-apical-initial cell. Fig. 12. L. S. of a foliar primordium indicating periclinal division of the sub-apical-initial cell. Also an anticlinal division can be noted in the adjacent cell. Note the discontinuity of the second tunica layer in the leaf primordium due to such division in the sub-apical cell. Fig. 13. L.S. of a primordium showing the six-celled sub-apical cell complex. Fig. 14. L.S. of a primordium showing the four-celled sub-apical cell complex. Fig. 15. Longitudinal section of a primordium showing the occurrence of periclinal divisions in two adjacent cells. Figs. 10–15, × 375.

FIGS. 16–21. Fig. 16. Transverse sectional view of a primordium at the time of marginal growth. Note the anticlinal and periclinal division of the sub-marginal-initial cell. Also the anticlinal and periclinal divisions of the abaxial and adaxial hypodermal layers are indicated. Fig. 17. T.S. of a developing lamina denoting the anticlinal division of the marginal-initial cell. Also a periclinal division of the abaxial hypodermal layer is represented. Fig. 18. T.S. of embryonic lamina showing the anticlinal division in the sub-marginal-initial cell and abaxial hypodermal layer and also in the marginal-initial cell. Fig. 19. T.S. of embryonic lamina showing the occurrence of periclinal divisions in the abaxial hypodermal layer. Fig. 20. T.S. of embryonic lamina showing the periclinal division of the sub-marginal-initial cell. Fig. 21 T.S. of embryonic lamina showing the presence of two sub-marginal-initial cells.

MI–Marginal-initial cell; SMI–Sub-marginal-initial cell; ABXL SIDE, Abaxial side of the lamina; ADXL SIDE, Adaxial side of the lamina. (All figures, × 375).

FOLIAR SCLEREIDS IN *MIMUSOPS HEXANDRA* ROXB.

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Introduction

The study of foliar sclereids is a subject of recent interest in India and confined mostly to the work of T. A. Rao (1947, 1948, 1950, 1951 *a*, 1951 *b*, 1951 *c*, 1952, 1953, 1954 and 1957), Subramanyam, K. and Rao, T. A. (1949), Rao, T. A. and Kelkar, S. S. (1951) and Rao, T. A. and Kulkarni, G. Y. (1952) and a few others. A detailed and systematic study of sclereids has also been taken up in this department and the present paper is one of the series and deals with *Mimusops hexandra* Roxb. a member of the Sapotaceæ.

Sclereids in *Mimusops* were reported by various workers so far back as 1908 (Solereder, 1908). Detailed studies of these sclereids particularly in *M. elengei* Linn. and *M. hexandra* Roxb. were made by D'Almeida and Desai (1942, pp. 26–27). Rao, T. A. (1950, p. 26) also recorded the presence of "irregularly branched sclerosed cells in close association with the veinlets", in *M. hexandra*, *M. elengei* and *M. roxburghiana* Wt.

The present paper is a more detailed study dealing with the ontogeny and the distribution of the foliar sclereids in *M. hexandra* Roxb.

Materials and Methods

The material for the study was collected from plants growing in the departmental garden. Both hand and microtome sections were examined. They were stained with three combinations: Safranin and Light green, Crystal violet and Orange G, and Hæmatoxylin and Orange G. In case of the last combination iron alum was used as a mordant, and this was found to be most suitable for ontogenetic studies. Whole mounts cleared in xylol were also examined. Maceration of the leaf was made by keeping it for about a day in concentrated nitric acid. Subsequently they were washed in water, dehydrated, finally cleared in xylol and mounted in canada balsam.

Microchemical tests were also used to find out the nature of the sclereid walls but without any satisfactory result.

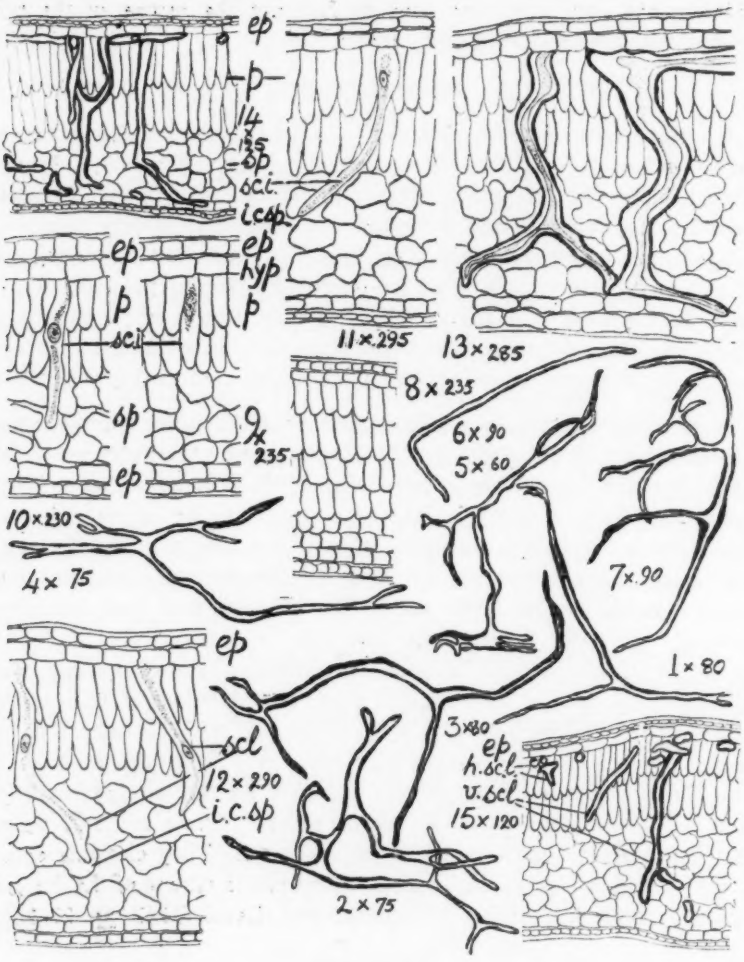
Distribution

A surface view of a cleared mount of a mature lamina shows irregularly branched sclereids scattered between the veinlets (Photo 1). Macerated sclereids appear as irregularly branched aseptate structures. Figures 1–7 represent a few forms assumed by the sclereids. But in very young stages they are simple and unbranched (Fig. 6). It appears that the division starts only at the ends and then becomes deeper leading to profusely branched types. But even the most highly branched types can be interpreted in terms of repeated dichotomy (Fig. 2). Sometimes this dichotomy is also accompanied by a little swelling of the sclereid in that region (Figs. 2, 5 and 7).

Further, the sclereids accompany the vascular bundles, almost surrounding them. Rao, T. A. (1950, pp. 26–27) comments, "A noteworthy feature of these fibres is their mode of branching at the end of veinlets. Near the veinlets they fork irregularly sometimes touching the larger veins or lie freely in the mesophyll. We notice that in our preparations the sclereids do lie freely in the mesophyll but their division near the vascular bundles or veinlets could not be made out." The sclereids and their branches are distributed not only horizontally but also vertically. Vertical sections (Figs. 13, 14, 15 and Photo 2) through the mature leaf show branched sclereids distributed in the mesophyll. Figure 13 shows two branched sclereids extending from the upper epidermis to the lower epidermis, with characteristic bends. Figures 14 and 15 show similar sclereids (*scl.*) in different stages of development. They also show some of the sclereids distributed horizontally but seen in a transverse section in the figures (*h.scl.*). These sclereids when old are thick-walled and have lumen of varying width. They elongate considerably and extend in some cases across the entire thickness of the lamina, as has already been noticed by D'Almeida and Desai (1942, pp. 27–28).

Ontogeny

The development of the sclereids was traced from the earliest stage of their formation. Very young leaves show no differentiation of the mesophyll or sclereids (Fig. 8). The cells of the mesophyll are compactly arranged with very little intercellular spaces between them. A transverse section of a young leaf with differentiated mesophyll (Fig. 9) shows certain large cells amidst the palisade parenchyma which are almost as long as the two layers of palisade tissue. This cell with thin walls, a large nucleus and full protoplasmic contents is the sclereid initial (*scl.i.*). It elongates gradually often



FIGS. 1–15. Figs. 1–7. Polymorphic mature sclereids of *M. hexandra* obtained by maceration. Fig. 8. Transection of young lamina showing undifferentiated mesophyll with compact arrangement. Figs. 9–13. Transections of young laminæ showing early stages in the ontogeny of sclereids. Fig. 9. Sclereid initial (*sc.i.*). Fig. 10. The initial has elongated and is pushing its way into the spongy tissue. Fig. 11. Obliquely elongated sclereid. Fig. 12. Sclereid showing bends and one of them shows beginning of a terminal dichotomy. Fig. 13. Mature sclereids with thickened walls, branched or bent and extending across the entire thickness of the lamina. The cell contents are still present. Figs. 14 and 15. Transection of old lamina showing sclereids cut longitudinally and transversely.

ep., Epidermis; *Hyp.*, Hypodermis; *H. scl.*, Horizontal sclereids; *I.C.sp.*, Intercellular space; *P.*, Palisade; *scl.*, Sclereids; *sc. i.*, Sclereid initial; *S.P.*, Spongy tissue.

forcing its way into the spongy parenchyma (Figs. 10 and 11). During this process the sclereid initial may become bent and may even show a tendency for apical dichotomy (Fig. 12). Still later stages (Fig. 13) show the fully elongated sclereid, dichotomised, twisted and extending from the upper to the lower epidermis. While some of the branches run vertically (Figs. 14 and 15, *v.scl.*), others run obliquely (*h.scl.*), spread themselves along the length and breadth of the leaf, often cross each other and thus form an intricate system in the leaf (*see* Photo 1). Some of the branches may even turn upwards again into the palisade (Fig. 14). Often, a sclereid forces itself between the epidermis and the hypodermis or amongst the layers of the spongy parenchyma (Fig. 14). The sclereids (*scl.*) retain their contents till a late stage of development although the walls become thickened. It is only when they are fully developed that the sclereids lose their contents and the walls become highly thickened although not stratified. Pit canals reported by earlier workers in *M. elengei* and *M. hexandra*, Rao, T. A. (1950, p. 27) could not be seen by us.

The above observations show that the sclereids in this species are definitely modified palisade parenchyma cells as in many other plants. The only possible function that these sclereids could serve would be to give the leaf a certain rigidity or mechanical strength. These sclereids can be put under the category *Asterosclereids* or "Branched sclereids" which are highly irregular in form and size (Tschirch, 1889, pp. 301–02). Rao, T. A. (1949, p. 28) classifies sclereids into four main groups on the basis of their ontogeny. His group II (where sclereids are mostly metamorphosed palisade cells) is subdivided into *Osteosclereids*, *Ophiuroid sclereids* and *Branching sclereids*. We agree with him that the sclereids of *M. hexandra* come under group two and type three. These branching sclereids also conform to the *Asterosclereids* of Foster (1942, p. 68) and Esau (1953, p. 213). According to them these sclereids arise from parenchyma either palisade or spongy by a process of secondary sclerosis.

Rao, T. A. and Kulkarni, G. Y. (1952, p. 56) point out that the sclereids in *Olea* sp. are branched more where the mesophyll is closely packed. To some extent this is substantiated by our observations on *Mimusops hexandra*. Intercellular spaces are also present in our material, but are few in number. The sclereids do not seem to avoid them, but they often penetrate into the intercellular spaces themselves (Figs. 10–12) as in many plants where sclereids are formed from parenchyma (Esau, K., 1953, p. 213).

The gradual transformation of these palisade cells into sclereids seen in *M. hexandra* is also reported in *Monstera* (Bloch, R., 1946), *Mouriria*

huberi (Foster, 1947), *Memecylon lushingtonii* (Rao, T. A., 1949), *M. heyneanum* (Rao, T. A., 1951 *b*), *Niebuhria apetala* (Rao, T. A., 1951), *Olea* sp. (Rao, T. A. and Kulkarni, G. Y., 1952) and *Linociera intermedia* (1958). Recently Rao, A. R. and Tewari, J. P. (1960) have shown that in *Codiæum variegatum* latex tubes become transformed into sclereids. This indicates that sclerization is an orderly process and is built on a definite pattern for each species. But the factors which govern this orderly process are not yet clearly known.

SUMMARY

Anatomical and ontogenetic studies of the foliar sclereids of *Mimusops hexandra* have been made. The sclereids are found to be modified palisade parenchyma cells which elongate, loose their contents and become thick-walled although the walls do not show any stratification. Adult sclereids are polymorphic and repeatedly branched. The branches run in the vertical as well as horizontal planes within the mesophyll.

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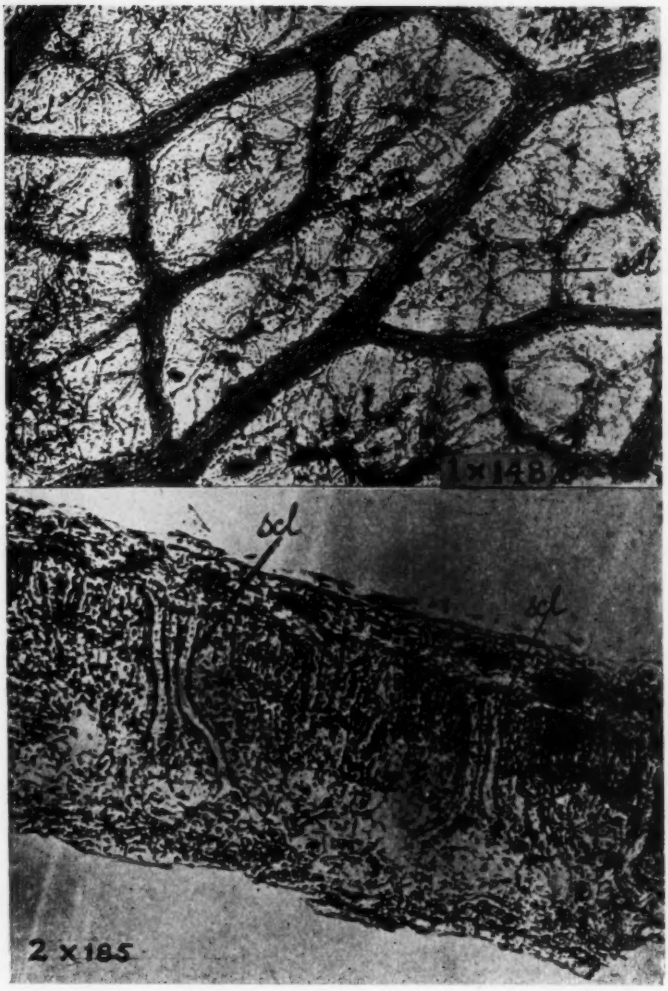

PHOTOS 1–2

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Explanation of Plate III

Photo 1. Part of cleared lamina of *M. hexandra* showing the sclereids (*scl.*) scattered between the veinlets (*v*), × 148.

Photo 2. Transection of *M. hexandra* leaf showing the mature vertical sclereids running across the entire thickness of the leaf, × 185.

THE REACTION OF THE NUCLEI OF THE VEGETATIVE CELLS AND ZYGOTES OF *SACCHAROMYCES CARLSBERGENSIS* TO SOME STAINING TECHNIQUES

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Introduction

The earlier observations on the structure of the zygote nucleus of yeast (Guilliermond, 1910; Winge, 1935; Badian, 1937; Lietz, 1951; Widra and DeLamater, 1955) show little agreement. They were all based on fixed and stained preparations without any reference to the structure of the living nucleus. There was no conformity even in the fixatives used. The presence of a nuclear membrane reported by Guilliermond was only surmised by the others.

The similarity in the structure of the nuclei of vegetative cells and zygotes suggested by Guilliermond was confirmed and extended for the first time by observations on living material (Thyagarajan and Subramaniam, 1957 *a*, *b*; Subramaniam, Royan, Thyagarajan, Aswathanarayana and Subramanyam, 1959; Thyagarajan, 1959). The reaction of the vegetative cells of *Saccharomyces cerevisiæ* NRRL Y-567 to many staining techniques (Royan, 1956, 1958 *a*, *b*; Royan and Subramaniam, 1960) and that of the vegetative cells of *S. cerevisiæ*, BY 1 (Aswathanarayana and Subramaniam, 1958) and the zygote of *S. carlsbergensis* (Thyagarajan and Subramaniam, 1957 *b*) to Heidenhain's hæmatoxylin and Feulgen have been investigated.

The vacuoles of vegetative cells and zygotes stain with neutral red (Thyagarajan, 1958). They are, therefore, cytoplasmic inclusions which need not figure in any discussion of the nucleus. From observations on hæmatoxylin preparations in which the vacuolar membrane had separated from the cytoplasm and lies free in the vacuolar area, the extra-vacuolar position of the nucleus has also been established (Subramaniam *et al.*, 1959).

A comparison of the reaction of the nuclei of vegetative cells and zygotes of *S. carlsbergensis* to some staining procedures under comparable experi-

mental conditions was, therefore, thought desirable to elucidate whether the 'nucleolus' reported by Guilliermond (1920) is a real nucleolus or whether it is a chromocenter (Royan, 1958 *b*; Subramaniam, 1960; Royan and Subramaniam, 1960).

Observations

The methods of culture and the procedures adopted for fixation have been described earlier (Thyagarajan and Subramaniam, 1957 *b*). The time of hydrolysis in N HCl at 60° C. or in 10% perchloric acid at 28° C. for the different types of staining are given in the legends for the illustrations.

Staining with Heidenhain's Hæmatoxylin.—By staining samples with hæmatoxylin, the minimum time required for optimal fixation in iodine formaldehyde acetic acid solution (IFA—Gram's iodine 9 ml., 40% formaldehyde 1 ml., glacial acetic acid 2 drops) was found to range from 45–75 min. The overall shrinkage of the cells was less when the fixation was limited to 60 min. Unlike in higher organisms, the intense cytoplasmic basophilia complicate the staining of the yeast nucleus with hæmatoxylin (Royan, 1956). This could be obviated by an extraction of the RNA by acid hydrolysis.

Photos 1–6 illustrate the variations in the structure of the nucleus of vegetative cells in hæmatoxylin preparations. It will be seen that the vacuoles appear unstained. The nuclear membrane appears very clear in Photos 2–5. The stained masses (Photos 2 and 3) often occupy almost half the area enclosed by the nuclear membrane. The membrane appears thickened in some regions in Micrograph 4 due to the plastering of intra-nuclear structures on it.

A pair of stained bodies lie close together in the nuclear matrix. Even in 7-day cultures where the majority are non-budding, a small percentage of cells have buds attached to them. Such an example is illustrated in Photo 5, where the nucleus of the mother cell lying near the bud has a stained crescent on one side. Two large stained structures are seen in the nucleus of the cell in Photo 6.

In spore zygotes, the nucleus lies free in the cytoplasmic band separating the unstained vacuoles. The structures inside the nuclei (Photos 7–10) occupy positions comparable to those in living zygotes (Thyagarajan, 1959) and in living and stained vegetative cells. The stained area may be large (Photo 7) or small (Photo 8). The nuclear membrane may be uniform (Photo 9) or may be irregularly thickened (Photo 10). In uni-vacuolar zygotes (Photo 11) the nucleus is usually located near the vacuole.

There is a remarkable similarity in the structure of the nuclei of vegetative cells and zygotes in hæmatoxylin preparations.

Staining by the Feulgen Technique.—A stay of two to three hours in leuco-basic fuchsin (Merck) was found to yield uniform results. The stained smears were passed through two changes of SO_2 water of 10 min. each, rinsed well in distilled water and tinted lightly with light green. Those intended for observation under phase contrast were not counterstained. The optimal time of hydrolysis was found to be 7-8 min. in N HCl at 60° C. and 5 hr. in 10% perchloric acid at 28° C.

Photos 12 and 18 are of an unhydrolysed vegetative cell and a zygote respectively, stained for the same duration as the hydrolysed ones. They exemplify the absence of any plasmal reaction. What is striking in hydrolysed cells is that the stained areas occupy only a portion of the nuclear matrix, whether it be that of vegetative cells (Photos 13–17) or zygotes (Photos 19–22). There is no fixity in the size, shape and location of these Feulgen positive areas inside the nuclei (Photos 13–17, 19–22). No difference was also observable in the reaction of the nuclei of a zygote and its bud (Photo 20) to the Feulgen stain. In both, the stained region occupies only a portion of the area enclosed by the nuclear membrane.

It is not difficult to visualize as to how the Feulgen stained area came to be identified as representing the whole nucleus (Winge and Roberts, 1954). The general invisibility of the nucleus in living cells combined with an entire dependance on the light microscope for interpretation of Feulgen preparations may have been responsible for such a conclusion. This is exemplified by micrographs taken under an ordinary microscope of Feulgen stained vegetative cells (Photos 13 and 14) and a zygote (Photo 19). The unstained areas of the nucleus as well as the nuclear membrane are invisible in these photos (13, 14 and 19).

Photo 20 of a zygote and its bud also taken under ordinary illumination gives a much better idea of the structure of the nucleus than Photo 19. But such pictures are likely to be ignored when no indication of the presence of the nuclear membrane is seen in the majority of the cells. A comparison of light (Photos 13, 14 and 19) and phase contrast micrographs (Photos 15–17, 21 and 22) of Feulgen stained vegetative cells and zygotes would show that the real structure of the nucleus is seen only when examined under phase contrast. Occasionally phase contrast micrographs also reveal Feulgen negative structures inside the nucleus. In Photo 22, for example, there are two crescentic unstained areas lying apposed to the inner surface of the nuclear membrane.

Not all the intra-nuclear structures seen in living and hæmatoxylin preparations are stained by Feulgen. From the reaction of the nucleus to the Schiff's reagent, it would appear that DNA is not uniformly dispersed inside the nucleus. The nucleus contains also Feulgen negative structures.

Staining with Giemsa's Solution.—The hydrolysed smears washed well in distilled water and stored in a phosphate buffer of pH 7·0 for 5–10 min. were transferred to Coplin jars containing 5 ml. of a Grübler or B.D.H. sample of the Giemsa stain diluted with 40 ml. of buffer. The staining of the nuclei could be observed after a lapse of 15 min. The smears were, however, left in the stain for 60–120 min. to obtain a deeper colouration. The nuclear details were clear when the staining had proceeded for 60 min. If the duration of staining was extended, the nucleus and the cytoplasm appeared densely coloured necessitating destaining with 20% alcohol prepared with buffer to obtain the proper contrast.

The photomicrographs presented are those of water mounts only since they showed greater detail than permanent ones (Royan, 1958 *a*). As can be seen from Photos 23–30 the vacuole is devoid of any stained structures. The nuclear membrane is distinct in all the cells though it is thin in some (Photos 26 and 30) and thick in the others (Photos 23–25). That it clearly delimits the nucleus not only from the cytoplasm but also from the vacuole is clearly seen in the bi-vacuolate cell shown in Photo 26 where the nuclear membrane is lying over one of the vacuoles. One (Photos 25, 27, 29 and 30) or more (Photos 23, 24 and 26) intra-nuclear bodies are stained by Giemsa. These may lie free in the nuclear matrix (Photo 23) or in close contact with the nuclear membrane (Photos 25–30). These bodies range in size from the small grain in Photo 29 to the irregular crescentic areas in Photos 26 and 27.

The nucleus of the zygote is located between the two vacuoles (Photos 27–29) and thus resembles in this respect the bi-vacuolate vegetative cells (Photo 26). Its location between the vacuole and the cell-wall in vegetative cells (Photos 23–35) appears to be the result of a shift in its position due to the enlargement of the vacuole, since in rare uni-vacuolate zygotes it is often found near the vacuole in the middle of the cell (Photo 30). While Giemsa is superior to Feulgen in revealing the nuclear membrane under ordinary illumination, it is inferior to hæmatoxylin in its utility for the study of the yeast nucleus in hydrolysed smears.

Discussion

The selection of a reliable fixative depends on the availability of the living nucleus for a study of its reactions and a fixative can be considered

reliable only when the details revealed on staining are superposable on those of living cells. It is in this context that IFA appears unique and has enabled a study of the reaction of the cells fixed in it to a variety of stains. The criticism against regressive stains in general (Nickerson, 1957) and hæmatoxylin in particular that "it produces a blurred and indistinct picture" (DeLamater, 1950) loses its force when the living nucleus is made the basis for comparison and the fixed smears are hydrolysed before staining to remove the cytoplasmic basophilia.

Generally, Feulgen preparations of cells fixed even in IFA do not give an accurate picture of the nuclear structure when examined under ordinary illumination (Photos 13, 14 and 19). The orientation of the intra-nuclear structures with reference to the nuclear membrane could be made out only when examined under a phase contrast microscope (Photos 15–17, 21 and 22). The photos would emphasize that DNA is not dispersed uniformly in the nuclear matrix (*cf.* Winge and Roberts, 1954). The nucleus of *S. carlsbergensis* has a diameter of 1·5–2·5 μ.

All the structures visible in the living nucleus could be stained with hæmatoxylin (Photos 1–11). But not all intra-nuclear structures are Feulgen positive. The nucleus encloses, therefore, chromocenters as well as nucleolar equivalents (Royan, 1958 *b*; Subramaniam, 1960; Royan and Subramaniam, 1960). Since Guilliermond (1910, 1920) based his observations mostly on hæmatoxylin stained preparations, it would appear that the body identified by him as the 'nucleolus' may either be the chromocenter or a nucleolar equivalent.

SUMMARY

Vegetative cells and zygotes of *Saccharomyces carlsbergensis* fixed in iodine formaldehyde acetic acid solution and stained after acid hydrolysis in hæmatoxylin, Feulgen and Giemsa show a remarkable similarity in the size and orientation of the structures in the nuclear matrix with reference to the nuclear membrane. The nucleolus described by Guilliermond may either be the chromocenter or the nucleolar equivalent.

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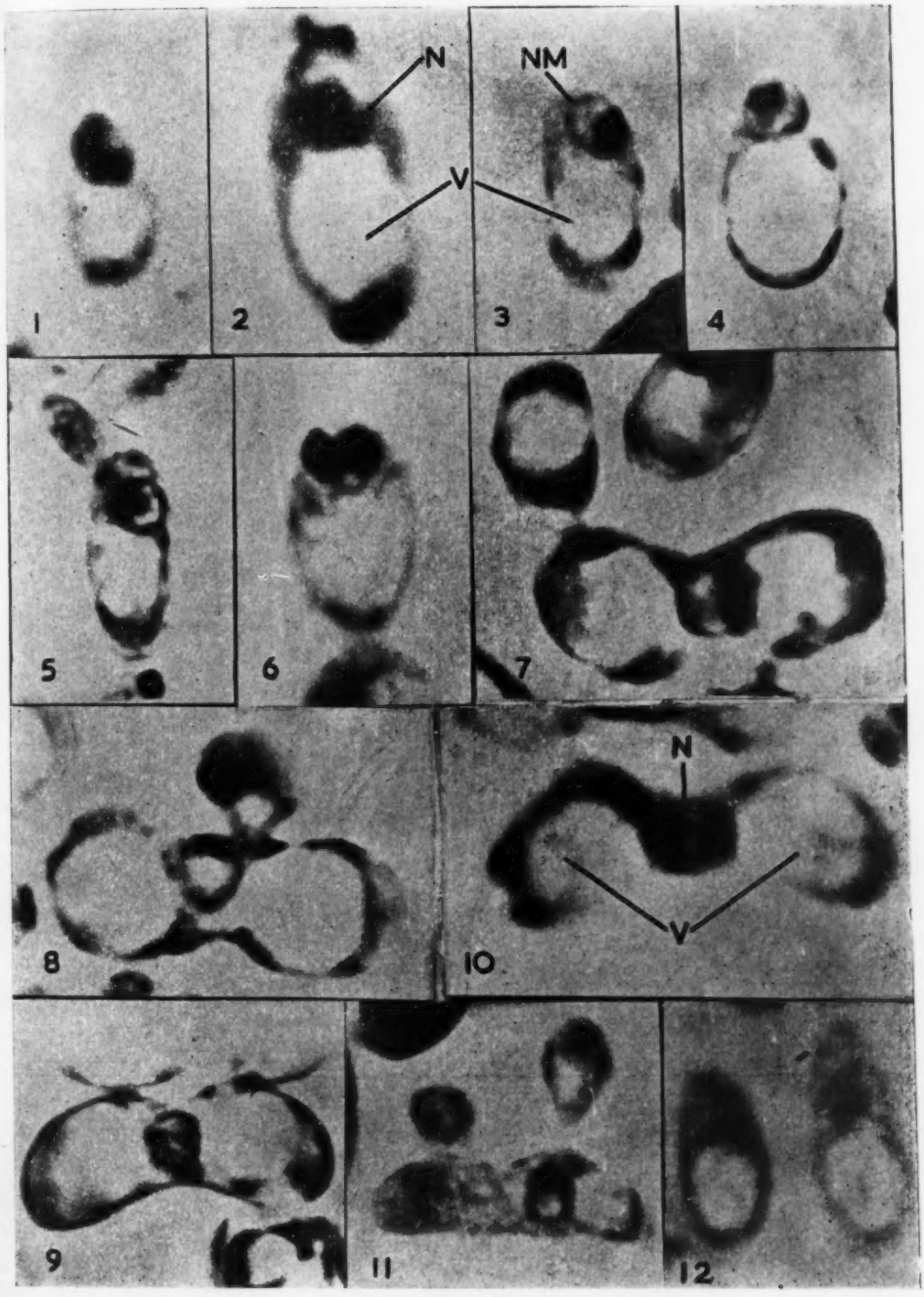
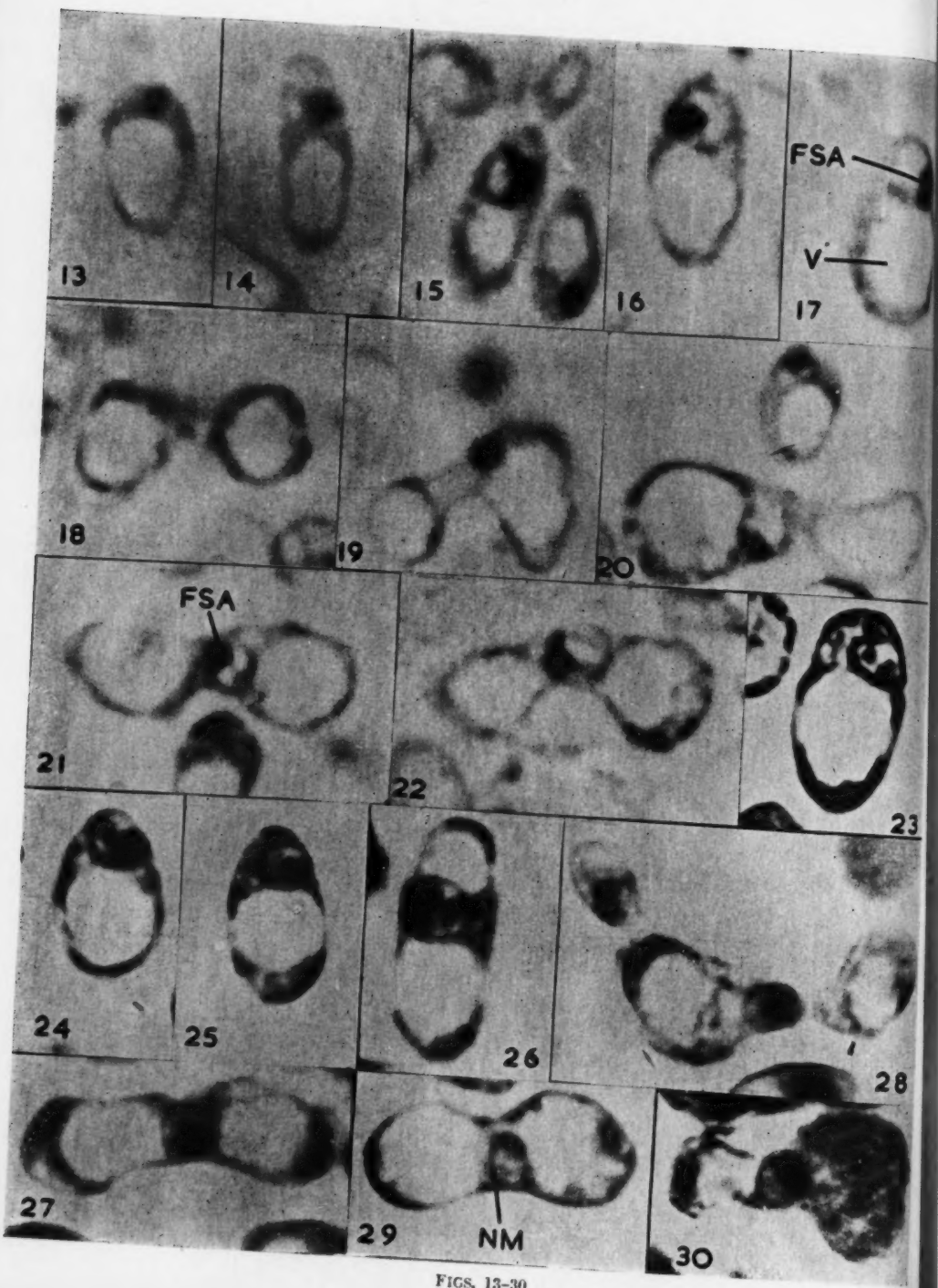


FIGS. 1–12



FIGS. 13–30

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Description of Photomicrographs

Plate IV

Photos 1–3, 5 and 6. Vegetative cells fixed in IFA for one hour, hydrolysed in N HCl for 8 minutes and stained in hæmatoxylin.

Photo 1. The stained area of the nucleus is crescentic in shape, × *ca.* 6,100.

Photos 2, 3 and 5. The nuclear membrane encloses stained areas. Photo 2. × *ca.* 8,700. Photos 3 and 5, × *ca.* 6,100.

Photo 4. A cell hydrolysed in 10% perchloric acid for three hours and stained in hæmatoxylin, × *ca.* 6,100.

Photo 6. Two large stained areas are seen in the nucleus, × *ca.* 6,100.

PHOTOS 7–11. Spore zygotes fixed in IFA, hydrolysed in N HCl for 8–9 minutes and stained in hæmatoxylin.

PHOTOS 7–10. The nucleus lies in the cytoplasmic band between the two vacuoles. Note the variation in the thickness of the nuclear membrane as well as the intra-nuclear structures. Photos 7 and 8, × *ca.* 7,200. Photos 9 and 10, × *ca.* 6,100.

PHOTO 11. A uni-vacuolate zygote with the nucleus located in the middle of the cell near the vacuole, × *ca.* 6,100.

PHOTO 12. Unhydrolysed cell stained in leuco-basic fuchsin and counterstained with light green. No plasmal reaction. Light microscope, × *ca.* 6,100.

PLATE V

PHOTOS 13–17, 19 and 22. Hydrolysed and stained in leuco-basic fuchsin, × *ca.* 6,100.

PHOTO 18. Unhydrolysed zygote stained in leuco-basic fuchsin and counterstained with light green. Light microscope. No plasmal reaction.

PHOTOS 13, 15–17, 19–22. Vegetative cells and zygotes hydrolysed in N HCl.

PHOTOS 13, 19 and 20. The Feulgen stained area. Light microscope.

PHOTO 14. Vegetative cell hydrolysed in 10% perchloric acid for five hours. The stained area is outside the vacuole. Light microscope.

PHOTOS 15–17, 21 and 22. The Feulgen positive areas are located inside the area bounded by the nuclear membrane. No counterstain. Phase contrast.

PHOTOS 23–30. Stained in Giemsa for one hour. Water mounts, × *ca.* 6,100.

PHOTOS 23–25, 27, 29 and 30. Cells hydrolysed in N HCl for 7–8 minutes.

PHOTOS 23–25. The nuclear membrane is distinct in all the cells and encloses stained structures.

PHOTOS 26 and 28. Cells stored in 10% perchloric acid for four hours. The nuclear membrane and the intra-nuclear bodies are clear.

PHOTOS 29 and 30. The stained patch inside the nucleus shows variations in size.

KEY TO LETTERING

N, Nucleus; NM, Nuclear Membrane; V, Vacuole; FSA, Feulgen stained area.

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TECTONICS WITH SPECIAL REFERENCE TO INDIA*

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ABSTRACT

The chief elements in the structure of the earth's crust are shield and stable areas (platforms), sedimentary basins; geosynclines, folded mountain ranges and the present mobile belts formed by compression; mid-ocean ridges, rifts and faults forming another group, due to tensional phenomena. Seismic and volcanic activities are associated with the folded and mobile belts as well as with the rifts. Both these types occur in a definite pattern. The compression phenomena are more or less confined to the Pacific margins and the Alpine-Himalayan belt of mountains on either side of Mediterranean. The tension rifts follow the middle of the Atlantic and Indian Oceans with branches going out into the South-Eastern Pacific and around Antarctica.

In the case of the mobile belts, the continental margins which were the loci of sedimentation were compressed, folded and thrust over the ocean side, forming circular arcs of various dimensions. This is very clearly seen around the Pacific Ocean. Though arcuate mountain chains are also found along the Alpine-Himalayan mountain belt, the former Mediterranean Ocean has largely disappeared by the continents coming together.

The mid-ocean ridges, particularly in the Atlantic and Indian Oceans, are broad mountain features which appear to have arisen from the stretching of the crust and extrusion of large masses of basic igneous material (Sima). Recent observations have shown that the middle of these ridges are marked by deep rifts with seismic and sometime volcanic activity.

India consists of a stable peninsular shield with a mobile belt around the whole of its northern border. The structure of the peninsula is controlled by the Dharwarian, Eastern Ghats, Satpura and Aravalli structural trends, which are responsible for the triangular pattern. The Aravalli belt extends north-east from Gujarat through Delhi to Garhwal. To its east is the great Vindhyan basin which is moulded on the Bundelkhand granite massif and which presumably extends also into the Sub-Himalayas of U.P. and Nepal. It is not yet known whether there is a

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continental nucleus in the centre of the peninsula. The structural trends have determined more or less the shape of the coast and also the direction of faulting of the three major troughs of coal-bearing rocks, one along the Damodar and Sone valleys, the second along the Mahanadi valley and the third along the Godavari valley. There is also a well-marked rift along the valley of the Narmada which has been a marine belt from the Permo-Carboniferous to recent times.

It is known that Madagascar was separated from East Africa in the Permian. The Mozambique Channel gradually widened, and from the Jurassic times marine strata were deposited, these being very closely related to the rocks of the same age found in Cutch, in the Baluchistan arc, and on the eastern side of Arabia. The eastern coast of India seems to have taken shape in the Upper Jurassic and there is a good marine succession from the Albian upwards. In Australia also there is evidence that its western coast was invaded by the incipient Indian Ocean in the Jurassic and more extensively in the Cretaceous.

The great fissure-eruptions of basic igneous rocks which occurred in Africa, South America and India (Rajmahal) in Upper Triasic or Jurassic times are apparently the manifestations of tension which resulted ultimately in the breaking up of the southern continents which constituted Gondwanaland. That the final break-up occurred in the early Cretaceous times is proved by stratigraphic data from the different parts of Gondwanaland but, as stated already, the incipient Arabian Sea seems to have opened up from Permian times which is also the period during which the Narmada rift was formed. Another great fissure-eruption occurred in Western India, Somaliland and Ethiopea in the Upper Cretaceous to Eocene.

The Alpine-Himalayan mountain ranges resulted from the compression and uplift of the great Equatorial Mediterranean geosyncline which existed during the Mesozoic era. The initial compression took place in the Upper Cretaceous when ultrabasic igneous rocks were intruded into the core of the mountain belt in Oman, in the Baluchistan arc and in the Himalayas as well as further east. The other major phases occurred in Upper Eocene, Lower or Middle Miocene and in the Plio-Pleistocene. These phases can be recognised over most of the Alpine-Himalayan belt though in varying degrees of intensity.

The rocks of the southern part of Indian Peninsula have a close connection with those of Ceylon, Madagascar and East Africa with which they are closely related structurally. This indicates that they all probably formed parts of one unit, with Australia lying on the one side and Antarctica on another. India began to drift away from the rest of Gondwanaland early in the Cretaceous by translatory motion as well as by anti-clockwise rotation through something like 60 degrees of arc. It

travelled far to the North and intensely crumpled up the Tethys basin and wedged itself into what is now Central Asia. The last is a region of numerous, more or less parallel, mountain ranges gathered up sheaf-like in the Pamir region. The ranges concerned are the Tien-Shan, Trans Alai, Kunlun-Lokzung, Altyntagh, Karakorum, Kailas, Zanskar and Himalaya from north to south. Their ages range from the Hercynian period in the north to the Alpine period in the south, the middle ranges having been affected by both of these revolutions, and perhaps also by the Cimmerian. All these ranges are characterised by high negative gravity anomalies which reach a maximum of a little over — 560 milligals in the Kunlun and Lokzung ranges. This indicates that there is a very great thickness of Sial in Central Asia, which is still a very disturbed region as indicated by the occurrence of earthquakes along these mountain belts. This region will ultimately attain equilibrium by a redistribution of mass which is now occurring as a spreading of the Asiatic continent to the east and south-east as indicated by the active island arcs of Kurile, Japan, Riukiu, Philippines, Banda and Sunda arcs on the inside and the Marianas-Yap-Palau and the Nias-Mentawei-Andaman arcs on the outside. The movement of India to the north-east was accompanied by the movement of Arabia also in the same direction creating the tension rifts of East Africa as well as the Red Sea rift. The Persian Gulf is probably of the nature of a *fore-deep* similar to the Gangetic plains, though it is continuous with the Mekran fault. Mountain building has presumably eased off around the northern borders of India, but as stated already it is still going on in South-Eastern and Eastern Asia. Perhaps even the spreading out of the Indian Ocean area is also still going on.

The deep penetration of India into Central Asia is indicated by the enormous compression evident in the Himalayan region as well as by the two spectacular hair-pin bends near Nangaparbat on the west and Nancha Barwa in the east. The Kashmir and the Assam wedges have gathered up the mountain ranges in the north-west and north-east corners beyond the Indian shield, these regions being highly seismic. Most of these facts about the tectonic features of India and its neighbourhood are best explained by the hypothesis of continental drift associated with the names of Taylor, Wegener and Du Toit.

General

THE earth's crust can be classified into a few major Tectonic units. These are the shield and stable areas (Platforms); sedimentary basins; geosynclines; folded mountain ranges or mobile belts; rifts and fault troughs and mid-ocean ridges. These units are essential elements in the structure of the globe and constitute the expression of the nature and structural history of the land and sea areas.

The *shield areas* are of Pre-Cambrian age and have remained more or less unaffected by folding movements since they were originally crystallised from a molten or semi-molten condition or were transformed by metamorphism of the pre-existing materials. They are the oldest land masses known at present. Their greatest age, indicated by measurements of the products of radioactive disintegration, is of the order of 3,000 million years. This must be taken as the most remote time the rocks formed in which have managed to remain essentially unchanged at a few places, though igneous and metamorphic activity has taken place elsewhere at later periods. The chief shield areas known at present are Central and North-Eastern Canada, parts of Brazil, Central and East Africa, Peninsular India, Western Australia, the Baltic region and part of Siberia.

The shield areas are often associated with ancient sedimentary areas which have attained more or less stability. These are generally known as 'Platforms'. The only disturbances which shields and platforms have been subjected to are vertical movements by faulting and rifting and also perhaps some loss along their margins by the sinking of fractured fragments. The erosion of these shields and platforms leads to accumulation of sediments in the ocean basins around them and ultimately these sediments may be folded and raised up into mountains.

The oceanic areas fall into two types of somewhat different characters; one is the Pacific basin with its unique characters, hemmed in almost entirely by folded mountain arcs converging upon it from all sides. The bottom of this ocean has no *sial* cover, being formed of a layer of *sima* (basaltic rock) ordinarily about 5-6 km. thick, directly overlying the mantle, and in turn overlain by 1–2 km. of sediments (Hess, 1959). This ocean basin is intersected by a series of fractures running E–W, NE–SW and NW–SE (Menard, 1959) along most of which basic volcanic materials have been extruded to form huge volcanic cones some of which rise to the surface. There are many other submerged flat-topped cones called 'guyots'. Some of these support coral islands and Atolls and are situated on certain well-marked 'swells', being thus different from the volcanoes found on anticlinal ridges of island arcs (Dietz, 1954). The individual blocks marked off by these major fractures are level plains but may be 2,000 to 5,000 ft. higher or lower than the adjacent blocks. The borders of these blocks show step-like scarps and terraces.

In contrast with the Pacific Ocean, the Atlantic and Indian Oceans are bordered by fractured and faulted coastlines. The geological structures of the lands surrounding them often terminate abruptly at the coasts. It

is thought that these oceans were formed by the breaking up of a former great continent, the fragments of which moved away from each other. The bottoms of these oceans may have a small thickness of sial overlying the usual simatic material. They are also characterised by the presence of large mid-ocean ridges lying roughly symmetrically between the land masses on either side. The mid-Atlantic ridge occupies the middle of the Atlantic Ocean right through and can be traced northward from Iceland through Spitzbergen to the mouths of the Lena river in Siberia, the whole of the course of the ridge being marked by volcanism and seismicity (Hope, 1959). At the other end it continues between Africa and Antarctica and joins the mid-Indian Ocean ridge in the region of Rodriguez through Prince Edward Island. The mid-Indian ridge in the north is the same as the Carlsberg ridge passing by Chagos and going on to New Amsterdam and St. Paul Islands. To its west are two concentric ridges. The more conspicuous of the two is the one on which Seychelles, Saya de Malha and Mauritius stand. Another narrow submerged ridge is shown in the bathymetric map of the Arabian Sea, between the two above-mentioned ridges, in the *Report of the John Murray Expedition* (Sewell, 1932). The mid-Indian ridge in the south branches off from near Rodriguez and continues as a broad feature to the east between Australia and Antarctica, joining the Easter Island-Galapagos ridge which occupies south-eastern Pacific basin. In the mid-Pacific is a continuous ridge system known as the Tuomotu-Christmas Island ridge and the mid-Pacific mountain range which first trends north-west and then west. From this a branch leads off in a north-westerly direction, marked by the Emperor Sea-mounts (Menard, 1958).

The mid-ocean ridges have in recent years been found to be huge mountain chains several hundred kilometers wide at the base and rising to various heights below sea-level. Indeed the mid-Atlantic ridge occupies one-third of the width of the Atlantic Ocean. At only a few places do the ridges come up to the surface as volcanic islands. By far the greater part of the mid-Atlantic and mid-Indian ridges are presumably composed of basic volcanic rocks. They may have been formed by the eruption of huge masses and simatic material through rifts which opened up perhaps repeatedly, as a result of stretching of the crust by the separation of the continental masses. It is now known that along their crest line there is a continuous and well-marked graben, often more than a thousand meters deep, occupied by basaltic or ultrabasic rocks and marked by earthquakes and volcanism throughout their length (Heezen, Tharp and Ewing, 1959). In the opinion of the writer these ridges owe their origin to tension which has riven the sial

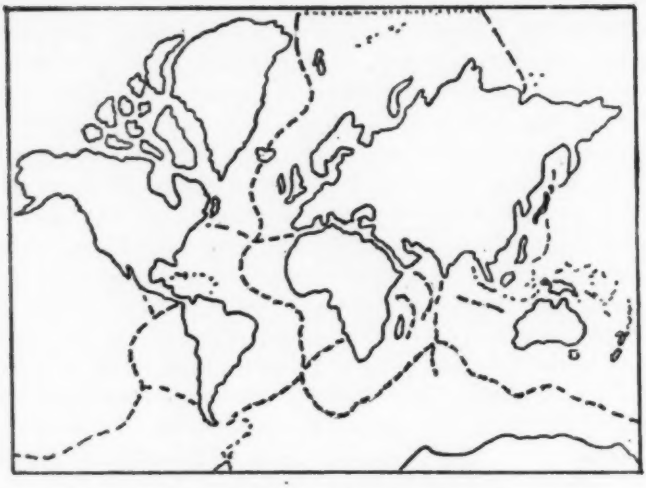

FIG. 1. Showing mid-ocean ridge systems of the world.

crust asunder, and brought up simatic material from below. The earthquakes in the mid-ocean ridges are all of shallow origin in contrast to those in the folded mountain belts surrounding the Pacific and along the Alpine-Himalayan belt where intermediate and deep focus earthquakes occur. They indicate that adjustments are taking place in these mid-ocean ridges at depths of 20–60 km. at the most. The fact that the gravity anomalies found over these ridges and rifts are moderate to small, indicates that isostatic equilibrium is comparatively easily reached along them, probably through the movement of magma in the zone below.

ISLAND ARCS AND TERTIARY MOUNTAIN RANGES

As already stated, the Pacific Ocean is surrounded by arc-shaped ridges mainly of Mesozoic and Cainozoic ages emerging out of the ocean one behind the other, often with an imbricate pattern. They show varying convexities, from almost straight ridges like the Tonga-Kermedec to those which have various curvatures and finally to sharply bent arcs such as the Banda and Antillean arcs. In all cases, the convexity is towards the Pacific Ocean except in the Antillean arcs and between Fiji and New Guinea around the Caroline basin. The general pattern of island arcs consists of the following units (Gutenberg and Richter, 1949):—

(1) A very deep narrow trench in the ocean; (2) a semi-emergent ridge coinciding with high negative gravity anomaly, adjoining the trench on the

continental side; this is the zone of shallow earthquakes; (3) the main anticlinal ridge with a volcanic zone on the inside; this is a zone of positive gravity anomalies and of earthquakes at about 60 km. depth, being situated some 150–200 km. behind the trench; (4) a second zone of volcanoes, extinct or showing decadent activity and sometimes earthquakes occurring at depths of 200–300 km.; (5) a sunken area or shelf sea with deep focus earthquakes. There are often combinations of certain zones and slight variations. The sunken land is generally of recent geological age. On the Asiatic side the arcs can be seen in various stages of development from the latest arcs which form the Marianas-Yap-Palau Island groups to those which are older like New Zealand, the Philippines and the Japanese Islands which are really parts of old continental borders, now separated from the continents by shallow seas. On the American side the arcs have been welded on to the continents, except in Central America where the Antilles arc faces the Atlantic and the Central American arc the Pacific.

The island arcs apparently indicate continental spreading—the annexation of the ocean by continental sial. Each arc represents sialic material from the continent expanding into the ocean. The shelf seas to the rear are in the meanwhile being filled with large quantities of sediments and are thus destined to become land. Indeed in some cases, the shelf seas were land at some previous time but had sunk to a shallow depth in response to adjustments taking place in the under-crust. There is one important distinction in the nature and composition of volcanic materials found in the Pacific Ocean on the one hand and in the land areas and island arcs on the other. The volcanoes on land and in the island arcs are predominantly andesitic, with subordinate basaltic, alkali and acid types. In the open Pacific the lavas are exclusively basaltic, with or without olivine. The great volcanic floods on land (plateau basalts) derived from fissure eruptions are also basaltic (mainly tholeiitic and more acid than ocean basalt). The outermost arcs in the Pacific from a well-marked petrological boundary known as the *Andesite Line* (Marshall, 1909; Hobbs, 1926). Two explanations have been offered for this demarcation; one is that andesite represents the contamination of basaltic material by sial through which the basalts pass on their way to the surface. The other view, due to J. T. Wilson (1954), is that the andesite comes from deeper down in the mantle and represents the partly differentiated material of the mantle from which the earth's crust has grown, separating ultimately into sial and sima. Perhaps there is some substance in both the views.

In all the island arcs, the island ridges represent the continental sial which is being thrust over a segment of the ocean; the oceanic crust, there-

fore, under-thrusts the continents in the opposite direction as visualised by W. H. Hobbs (1941). This is generally believed to result from convection currents in the mantle. Compressive forces are set up along the continental margin where the current takes a downward plunge, the upward direction of flow of the returning currents being under the continents themselves.

Only a short segment of the Pacific front shows concave arcs (ignoring for the present the complex Celebes arc which is concave towards the head of New Guinea), namely the Fiji-New Hebrides-Solomons, New Britain and New Guinea arcs. Gutenberg and Richter merely state that the Solomons and New Britain have their convexity *in an unusual direction* (1949, p. 50). The curvature of these arcs and the distribution of earthquake foci indicate a southward thrust of the superficial crust of the Ellice-Gilbert-Caroline block over the Tasman Sea, which in turn is being overthrust eastward over the New Zealand-Tonga-Fiji salient. The deeper shocks associated with the above-mentioned arcs are found on the Pacific side of the arcs whereas in every other island arc, including the Tonga-Kermede arc, the intermediate and deep-focus earthquakes occur on the continental side. But in every case without exception, the deeper earthquake belt occurs on the concave side of the arc.

The formation of *island arcs* appears to be the normal mode of continental spreading or growth. This is certainly the case in the Pacific border where Hercynian, Cimmerian and Laramide orogenic episodes are recognisable in the arcs, the later arcs appearing successively more on the ocean side. It may be expected that the same arrangement holds for the equatorial Alpine-Himalayan belt where mountain ranges have been developed on the borders of the Mesozoic Mediterranean Sea (Tethys). But it is rather difficult to recognise and disentangle the mountains of various ages because the land masses have met and there has been considerable uplift, over-thrusting and intermingling of strata. Most of the arcs in this belt have their convexity to the south, the Alps forming an exception. The various units are—the Burma arc which is a continuation of the Indonesian and Andaman arc; the large Himalayan arc which is continued to the west by the Baluchistan and Zagros mountains; the Taurus arc of Turkey which continues westward into the Pindus mountains of Greece and the Dinaric Alps of Yugoslavia; then the Apennines going into the North-West Africa as the Atlas mountains. There is a second series of arcs practically all along, which may represent the opposite border of the former Mesozoic sea and may also include a Mesozoic Orogenic element. This second series comprises the Pyrenees, the Alps, the Carpathians in Europe; further east the Caucasus and the Elburz mountains which continue into the Hindukush

and Karakorum mountains whose extension is to be found in Tibet and South-West China. Arkell (1956) has shown that the Caucasus and possibly the Elburz mountains are mainly of Cimmerian age and that they were later affected by the Himalayan movements also. De Terra (1936) considered the Karakorum mountains to be mainly of Hercynian age, but they are likely to include an element of Cimmerian orogeny also. Along some parts of these various ranges, it is possible to recognise the former existence of island arcs only in a vague manner because most of the original structures have disappeared in the great thrust movements of later age. In the Himalayan Tibetan region the original sedimentary basin has been subjected to the most intense compression imaginable because of the direct impact of the continental masses from both sides whereby the most complex structures have been produced, involving overriding, overturning, vertical thrusting and horizontal translation.

Tectonics of India

The Peninsula of India is a stable mass (shield) which has been free from folding movements since the end of the Pre-Cambrian times. It has, however, supported epi-continental seas in the late Pre-Cambrian and early Paleozoic, resulting in the deposition of sediments of Cuddapah and Vindhyan age. There are three areas of late Pre-Cambrian and early Paleozoic ages in the Peninsula, *viz.*, the Cuddapah basin in the south, the Great Vindhyan basin in Central India and U.P. and another large area in the north-eastern part of the Peninsula. The last has, however, been fragmented into a number of patches by erosion and removal. The Cuddapah basin is found to have a crescent shape with the concave side towards and parallel to the east coast, along which there has been some shearing and thrusting in Post-Cuddapah but Pre-Vindhyan times. Similarly, there has been some movement also in the Vindhyan basin, particularly on its western margin, where Pre-Cambrian rocks of the Aravalli belt have been thrust over its edges (Krishnan, 1953).

The Peninsula shows certain major structural trends which have a rough triangular pattern. The oldest of these is that of the Aravalli mountains which extend from Cambay in Gujarat through Delhi into Garhwal in the Sub-Himalayan region. This structure is found to splay out in the south; it is very likely that it continues partly into the Dharwar-Mysore region. The Aravalli trend has a NE–SW direction and the region shows orogenic disturbances of at least two ages, the earlier one affecting the Aravalli formations, and the younger one involving also the Delhi formations which overlie them more or less along the same belt. This trend

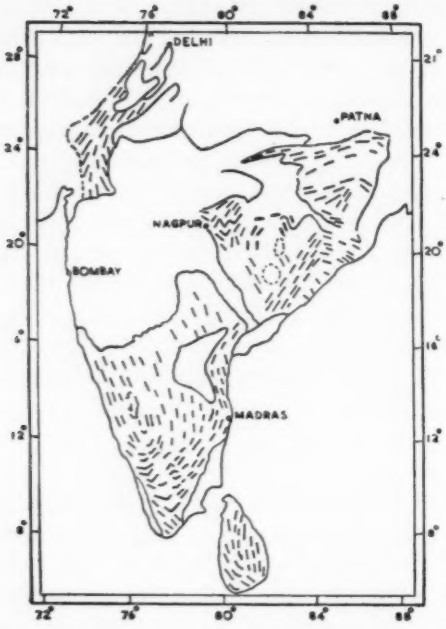

FIG. 2. Structural trend lines in the Archæans of Peninsular India.

continues into Garhwal in the Himalayas where it has escaped destruction probably because it is parallel to the direction of the forces which produced the Himalayan movements (*i.e.*, perpendicular to the strike of the Himalayan folds and thrusts). Coming to the Mysore region, we find that the rocks of the Dharwarian system have a general NNW–SSE strike, consisting mainly of strips of schistose rocks folded in with the Peninsular Gneiss. This trend continues to the south of Mysore city where it appears to blend with Eastern Ghats structure which comes in from the east. The southern part of Mysore shows rocks of higher grade metamorphism than the northern part, this being due to an upward tilting of the rocks in the south which has brought rocks from deeper zones to the surface. The ages determined for galena from Chitaldrug and for monazite from a pegmatite near Bangalore show 2,600 and 2,400 million years respectively (Holmes, 1954).

The eastern border of India contains rocks having the trend of the Eastern Ghats which run parallel to the coast from the Mahanadi valley down to Krishna valley in a S-W direction and then follow the eastern edge of the Cuddapah basin down to Madras where they turn to the south-west and proceed through Arcot and Salem into the Nilgiri mountains. Though

the Eastern Ghats comprise somewhat heterogeneous lithological elements, they have some structural unity. Near the Krishna valley the trend seems to spread out and a part strikes out slightly east of south into the sea and is found to continue into Ceylon. This island consists of rocks of typical Eastern Ghats facies forming a big synclinal fold with a nearly N–S axis. In South-Western Ceylon there are structures which are aligned in the direction of the southernmost part of the Indian Peninsula, namely, Travancore. It is probable that Travancore and the southern districts of Madras belong to the Eastern Ghats Province in which some later rocks may have been incorporated. Age data are available only for some Monozites and Cheralite of Travancore which give ages ranging from 490–650 million years. These apparently belong to late granitic rocks formed in the Upper Pre-Cambrian and in the early Cambrian era. This region also does contain more ancient rock groups including Charnockites and schistose rocks which still await investigation. Several pegmatite minerals from the Eastern Ghats belt from Nellore, Visakhapatnam and Orissa indicate ages around 1,550–1,800 million years (Mahadevan and Aswathanarayana, 1955; Aswathanarayana, 1956). The Eastern Ghats were considered by Fermor to be a range rejuvenated after they were originally formed, because their typical rocks, the Charnockites and Khondalites, bear the impress of deep-seated metamorphism. They also appear to cut through other rocks having a different trend which occupy the coastal region and the hinterland. At their north-eastern end, the trend of the Eastern Ghats veers round to the east where it ends abruptly at the coast. It is an interesting fact that rocks similar to those of South India, including the Charnockites, Dharwars and Cuddapahs, are found in Western Australia which may have originally lain close to the eastern part of India. The hinterland of the Eastern Ghats is not yet sufficiently known but it seems to contain rock formations with N-W as well as N-E trends.

The northern edge of the peninsular mass in Northern India is marked by yet another major trend which has an ENE direction. This has been designated as the *Satpura trend*, after the Satpura mountains which border the Narmada valley in Western India. This belt splits up into two branches, the northern branch going through Jabalpur and the Sone valley to the north of the Ranchi plateau, while the southern one passes through the manganese and iron ore-bearing region of the Central Provinces, Gangpur and Singhbhum, extending down to the Eastern Ghats north of the Mahanadi valley. In Bihar, the two branches are separated by the huge batholithic granite mass of Ranchi-Hazaribagh-Gaya. The Satpura trend continues into the Assam plateau across the Rajmahal-Garo gap through which

the Ganges and Brahmaputra rivers flow south to their delta. The age of some of the pegmatites of Gaya in this belt is around 950 million years. The Satpura belt rocks appear to be intermediate in age between the Eastern Ghats rocks and the post-Delhi pegmatites of Rajasthan which indicate an age of about 730 million years. Suitable materials from other localities in this area await investigation (Krishnan, 1953).

PROMINENT WEDGES OF THE PENINSULA

The Assam plateau is without doubt a part of Indian Peninsula but it is now isolated from it by the Ganges delta. Its rocks are very similar to those of Bihar and Orissa. The ancient rocks become covered by Tertiary formations beyond the Mikir Hills in Upper Assam but they presumably extend far to the north-east as a wedge. The presence of this wedge has been responsible for the sharp hair-pin bend of the formations at the eastern extremity of the Himalayan mountains east of the peak Namcha Barwa. On either side of this region, the rocks have nearly a NE-SW trend. On the Indo-Burma border they gradually swing to the south and follow the frontier to the Arakan coast and then go into the East Indies through the Andaman-Nicobar Islands. Attention may also be drawn to certain other features like the high seismicity of the Sikang region (S-W China) with its succession of mountain ranges. Though this is one of the least known regions of the world, there is little doubt that it is similar in structure to the Pamir region at the other end of the Himalayas. All the great rivers of South-East Asia rise in this region—Zayul and one or two other tributaries of the Brahmaputra, the Chindwin, Irrawaddy, Salween, Mekong, Chin and Yalung (Yang-tse-Kiang). In this region they all flow along neighbouring, close-set, parallel gorges within a few miles of each other, in a south-east and then southerly direction for over 250 miles before they diverge and fan out in different directions to their destinations which are spread between Dacca in East Pakistan at the head of the Bay of Bengal and Shanghai on the East China Sea to the south of Japan.

There is a similar wedge or rather a series of wedges on the north-western side of the Peninsula. The most impressive of these is the Punjab-Kashmir wedge which seems to be under-thrust to a great distance below Kashmir into the region of the Pamir mountains. The Himalayan ranges of U.P. and Punjab have a north-west direction and the geological formations execute a very sharp hair-pin bend near Nangaparbat and turn round to the south-west and south (Wadia, 1931). Several mountain ranges are gathered up in the Pamirs wherefrom they spread out towards the east, south-east, west and south-west. From north to south they comprise the

Trans-Alai, Kun Lun, Hindukush–Karakorum, Trans-Himalaya, Kailas and the major Himalayan ranges. In Hazara in the North-West Frontier Province, some ranges branch off towards Afghanistan while others proceed to the south and south-west. The major ranges bordering the Indus Valley are the Sulaiman, Laki and Kirthar. There are two subsidiary wedges of the Peninsula, one near Dera Ismail Khan and the other near Quetta, where also their effect is clearly seen in the gathering up of the formations into well-marked festoons which finally spread out in the Makran region of Baluchistan and turn round to the west to continue into Southern Persia and the adjacent Oman region of Arabia.

As already mentioned, the apical regions of wedge-like prominences are tectonic features showing high seismicity. The Pamir region is known for its numerous large earthquakes at depths of about 200–230 km. (Gutenberg and Richter, 1949). The Quetta region is also similarly visited by frequent earthquakes though these have shallow foci. The whole of peninsular border, occupied by the Himalayan and allied arcs, is of course a well-marked seismic belt indicating that the mountain building activity has not yet completely died out.

The Coasts of India

There is definite geological evidence that the eastern coast of India took shape in the Upper Jurassic or in the earliest Cretaceous. At several places along this coast, from Ramanathapuram (Ramnad) and Tiruchirapalli (Trichinopoly) in the south to the Mahanadi valley in the north, there are patches of Upper Gondwana sediments which are generally assigned a Jurassic age as they are correlated with the Rajmahal plant-bearing strata. At some places, particularly in the Guntur District, these strata are associated with marine formations which have yielded a few fossils whose age has been determined as Lower Cretaceous. It may, therefore, be stated that, by the early Cretaceous, the coast had taken more or less its present shape, and later in the same geological period there were large marine transgressions in the South Arcot–Tiruchirapalli region in the south and along the southern border of the Assam plateau in the north. The Cretaceous rocks on the Bay of Bengal side have a very close resemblance in facies and fauna to those found along the coasts of East Africa, Madagascar and Natal as also of Western Australia.

The western coast of India seems to have been evolved in two or more stages. It is known, however, that in the Permo-Carboniferous times, an arm of the Tethys extended southwards from Arabia over Eritrea towards East Africa, this period being marked by lagunal sediments indicating the

formation of a shallow sea. Somewhat later the region of the present Mozambique channel appears to have opened up, separating East Africa from Madagascar. About the same time there was established direct marine connection from Baluchistan over Cutch to the Mozambique Channel. By the beginning of the Jurassic, this channel had become large enough to enable marine deposits to be laid down in along the western coast of Madagascar and in Cutch and S-W Rajasthan. It is interesting to note that along the Narmada valley there are small patches of marine Permo-Carboniferous rocks at Umaria and one or two other places near about in Central India, which indicate that there was an arm of the sea along this belt. A small area of Permo-Carboniferous rocks has also been found in North-Western Australia, containing a fauna similar to that of Umaria (Dickins and Thomas, 1958). A large part of the Narmada valley belt is now covered by the lavas of the Deccan Trap and by later formations, which naturally obscure what is underneath. It is almost certain that the Narmada valley was an inlet of the Tethys sea which entered here from Rajasthan and Cutch which are now occupied by marine Jurassic deposits. These Cutch deposits have extraordinarily close resemblances to those of Madagascar, East Africa and the Punjab Salt Range in their lithological characters and fossils. The Narmada valley depression was partly filled by the Deccan Traps but seems to have persisted till recent times, for in the Valley of the Purna which is a tributary of the Narmada, we know of the existence of fairly thick Pleistocene deposits.

There are also three important fault troughs in Peninsular India, now marked by the presence of coal-bearing formations. These coal formations must originally have occupied much larger areas but have been preserved from denudation by having been faulted down sometime after their deposition. These troughs are occupied by the Damodar-Sone valley, the Mahanadi valley and the Godavari valley. It is not unlikely that the Narmada rift connected with the Sone and Godavari rifts. They are parallel to the regional strike of the basement rocks on either side of them, and are fundamental features in the structure of India. It is now known that there are faults roughly parallel to the western border of the Ganges delta, for the Rajmahal Traps which crop out on the Rajmahal hills at the head of the delta are found at progressively larger depths in a south-easterly direction (over 10,000 ft. deep near Burdwan).

On the eastern border of the Aravalli belt there is a well-marked thrust zone which is known as the Great Boundary Fault of Rajaputana. It has been traced over a distance of more than 500 miles along the Chambal valley where the older rocks of the Aravalli belt have been thrust over the Vindhyan

formations of the Great Vindhyan Basin. The age of this fault is not known but it may be contemporaneous with the Hercynian movements.

The Indo-Gangetic Plains

These plains occupy a depression in front of the mountain belt of the Himalayas and its associated ranges. The borders of the Indian continent have evidently been bent down and thrust under the mountains. This depressed zone, therefore, forms a "fore-deep". Recent aero-magnetic data indicate that, near the front of the mountains, the fore-deep contains a vast thickness of sediments of the order of 25,000 ft. or even more, lying over the basement rocks. The thickness decreases gradually on in a southerly direction towards the Peninsula. These sediments may include the whole Mesozoic and Kainozoic succession and may contain some oil-bearing structures where the rocks have not been too much disturbed or fractured.

The Extra-Peninsula

The region bordering India and its north, north-east and north-west constitutes the Himalaya mountains and associated chains. Of these, the Himalayas proper represent a region of tremendous crustal shortening in which a vast thickness of sediments, which must originally have occupied a great width of marine basin have been compressed and raised up to form a series of more or less parallel mountain chains between the borders of India in the south and the Kun Lun mountains in the north. The Himalayas are usually divided longitudinally into four zones. The southernmost is the *Siwalik Zone* which contains coarse sediments of the "molasse" type formed by the rapid denudation of rising mountains after the major uplift had taken place in the stage of mountain building. To the north of this zone are the *Lesser Himalayas* consisting mostly of non-fossiliferous sediments, whose age is difficult to determine but part of which must in any case have been deposited along the borders of the Indian shield. Beyond this comes the *Central Himalayan Zone* with high peaks and batholithic granite intrusions. These two zones are marked by enormous thrust sheets in which the rocks are often crumpled, inverted and over-ridden by older rocks from the north. Beyond the zone of high peaks is the *Tethys-Himalaya* which shows a magnificent series of fossiliferous sediments of all ages up to the earliest Tertiary. Farther on are the Ladakh and Kailas ranges, followed by the Trans-Himalaya range. As we proceed further north the successive ranges tend to become more straight. The more northerly ranges are also of earlier geological age. The Kun Lun and Karakorum ranges are of

Hercynian and Cimmerian (Jurassic) ages whereas the Tien-Shan ranges further north are entirely Hercynian or even partly earlier.

Central Asia is well known for its high altitude averaging about 12,000 ft. to 14,000 ft. above sea-level. In spite of this great altitude, this region shows negative gravity anomalies almost everywhere, and particularly along the various mountain chains. There are indeed a series of parallel zones of negative gravity anomalies in which high and low anomalies alternate. The highest negative anomalies (Bouguer) in the whole world (so far as I am aware) occur in the eastern part of the Kun Lun mountains, and the Lokzung Range where they attain a value of over −560 milligals (Norin and Ambolt, 1950). Even the old platform to its north, known as the Tsaidam depression, shows negative anomalies of the order of −50 to −100 milligals. It is obvious, therefore, that in this region an enormous thickness of sediments and granitic materials must be present.

Woollard has attempted to show the general relationship between Bouguer anomaly and the crustal thickness (depth to Mohorovicic discontinuity). The plotting of the values, using both earthquake wave velocities and quarry blast velocities, showed a good deal of scatter of points (Woollard, 1959, pp. 1530, 1542). Extrapolation of the curve for the maximum magnitude of the Bouguer anomalies indicated above would give a crustal thickness of the order of 75 km. which does not appear to be excessive for the conditions in Central Asia.

To the east and west of the Himalayas are the Burma and Baluchistan arcs respectively. The Burma arc is a single large circular arc which continues in an unbroken line through the Andamans and other islands of the Indonesian Archipelago. It is a mountain formed at the same time as the main Himalayan chain, namely, in late Cretaceous (Laramide) times. The central ridge in the south exposes Cretaceous and Tertiary rocks but in the north there are evidently older rocks to be found, though their distribution is not known because of the great inaccessibility of the territory. When this ridge was formed, the original sea occupying Assam-Burma was split into two arms, the eastern one in Burma showing a complete Tertiary succession with comparatively gently folded strata. This Tertiary basin contains a number of oil-fields which are being exploited at present. It also shows a volcanic line in which volcanoes have been active in the Upper Tertiary and recent times. This line lies just to the east of the major arc and parallel to it and is marked by Barren Island, Narcondam, Mount Popa, etc. It continues into the volcanic zone of Sumatra and Java and other islands. To the east of the Tertiary belt of Burma is the Shan-Tenasserim belt con-

taining Palæozoic and Mesozoic rocks belonging to the Cathasiyan Province which have become welded on to the Burmese arc after the rise of the Himalayan mountain chains. The age of mountain building and uplift of the Shan belt is the Cimmerian (Nevadan) of middle or upper Jurassic age. This belt, which is marked by much granitic material, passes through Malaya, the Tin islands of East Indies and Central part of Borneo and finally into Northern Philippines. A good part of it is known to be rich in tin and tungsten deposits.

On the other side of India we have the Baluchistan arc made up of three or four short subsidiary arcs, presumably because of the presence of wedges of the Peninsula which have been thrust under the mountain belt and have produced festoons. The apices of these wedges are in the region of the western end of the Salt Range, near Dera Ismail Khan and near Sibi-Quetta. The northern part of this arc which traverses Hazara-Kashmir and the N-W Frontier Province shows two distinct marine facies lying side by side, the western one being very closely allied to the Tethys-Himalaya and the eastern one characterised by Calcareous rocks and hence designated the *Calcareous Zone* of Baluchistan. The Tethyan facies apparently continues in a westerly direction into Afghanistan. The Calcareous zone, particularly in the southern part of the North-West Frontier Province and in Baluchistan, does not show rocks older than the Permo-Carboniferous. This arc becomes much broader in Makran and continues westwards into Persia where it forms Zagros Mountain belt. The Kirthar Mountain range, which forms the boundary between Sind and Baluchistan, strikes into the sea near Karachi but turns to the WSW and continues under the Arabian Sea as a series of sub-parallel sub-marine ridges and ultimately merges into the Oman ranges in Eastern Arabia. The Oman Mountains are known to have been formed in Upper Cretaceous times and are therefore a continuation of the Sind-Baluchistan ranges. They are undoubtedly a branch of the Zagros ranges which they leave near the kink at the entrance of the Persian Gulf, the Oman structure being attributable to the overthrust of a small part of the marine basin over the Arabian shield to its west and southwest.

The Himalayas were uplifted in four major impulses; the first period of compression and uplift was in the Upper Cretaceous as clearly indicated by the shallowing of the Upper-Cretaceous seas and also by the presence of ultrabasic intrusives and radiolarites in the root zone of the mountains. The second period of mountain building was in the Upper Eocene when the ocean basin was split up into long narrow shallow strips. The deposits formed after this movement are the well-known Murrees which have the

character of 'flysch' sediments, derived from the rapidly rising mountains partly even by sediments gliding down the slopes. The third period of disturbance was in the Lower Miocene which also was apparently a period of great uplift and igneous intrusion. After this uplift, all bodies of water disappeared entirely from the Himalayan region and the newly risen mountains together with the closely associated intrusive granitic rocks gave rise to coarse clastic sediments of 'Molasse' type known as Siwalik formations. Movements also took p'ace later, in the Pliocene-Pleistocene. De Terra (1936) records that uplift took place in the Western Himalayas even after early man had appeared. It is known that Pleistocene sediments occupy tilted positions on the flanks of the Pir Panjal range in Jammu-Kashmir and there are abundant evidences of early human culture during the Second Interglacial period.

It will be noticed that all the mountain chains surrounding India along its northern, north-eastern and north-western borders have their convex sides facing India and *the rocks have been thrust towards India from outside.* This simultaneous thrusting from all sides is possible only if we envisage the drift of the Indian continent into the area occupied originally by the Tethys Sea. Other features in the Himalayas and the neighbouring lands are also explained by the assumption that the Indian continent has thrust back the whole of the marine belt to a considerable distance to the north. It is obvious that these sediments of the Tethyan basin have undergone very great compression and have been raised to the greatest heights ever attained by mountains on land, about 29,000 ft. or nearly 9 km. Aa a result of such compression, rocks of certain facies, almost identical with those of the Dachsteinkalk and Hallsfatt marble of the Eastern Alps, which are exposed in some thrust sheets, are not to be found *in situ* in the basin, for they have undoubtedly been submerged under the huge piles of other sedimentary facies and zones. Compared to the compression in the Himalayan belt, the compression on the two flanks of India is much less intense, as can be readily understood.

The compression and raising up of the Tethys basin is considered to be the result of the drift of India from south to north. The drifting of India began presumably from early Cretaceous times up to which it was attached to Madagascar (and the Southern Continents). The early Cretaceous faulting of the eastern coast of Madagascar is attested by the fact that it is a straight faulted coast and its earliest marine strata are of Lower Cretaceous age. On the western side of Madagascar, however, a depression had begun to form in the Permian. It became part of a deep open sea only in early Jurassic, after which a well-developed marine succession appears. Similar

Jurassic marine strata appear in the adjacent Kenya coast as also in Cutch in India, all these having almost identical fossil species and zonal succession. It is, therefore, clear that an arm of the Tethys extended south-west from Baluchistan to the Mozambique Channel, which gradually widened after the Permian. That sea extended further along the east coast of South Africa in the early Cretaceous times and reached Argentina. The great similarity of the Pre-Cambrian rocks of the southernmost part of India, Ceylon, Madagascar and East Africa supports the idea of all these having been parts of a large land mass. The structures are also conformable if India is placed by the side of Madagascar and the latter close to East Africa as was presumably the case in the early Mesozoic. It is also possible that India's neighbour on its east was Australia. The Pre-Cambrian metamorphics and sedimentaries in the two countries have much in common.

The relative drift of India from Africa seems to have taken place in four or five stages, each major impulse being separated from the next by a period of comparative quiescence. The major line of separation in the crust should be taken as the Carlsberg-Mid Indian Ridge, the median rift in which is continued north-westwards by the Gulf of Aden and the Red Sea. The Red Sea is a wide rift underlain by basic igneous rocks showing positive gravity anomalies of 50–150 milligals. It is 300–400 km. wide and has a depth of about 2,000 metres. The African rift valleys are much narrower and shallower though their features are of the same type and are marked Tertiary volcanic rocks showing negative gravity anomalies of 50–100 milligals (Girdler, 1958).

According to Tromp (1950), the Red Sea region was domed up in the Eocene prior to its breaking up in early Oligocene, and was gradually widened to its present dimensions at a later age. The physiography of the region clearly shows that shearing movement (left-handed) has taken place in addition to simple rifting. It is bordered on both sides by parallel faults along which volcanic phenomena have been manifested in the later Tertiary, this being particularly well seen on the Arabian side. The positive gravity anomaly of the Red Sea is to be attributed to the large size of the rift which permitted the free movement of magma from the basaltic layer which has occupied the bottom of the rift.

The delineation of the African rift valleys, the Red Sea, and the Dead Sea rifts in Palestine are all genetically collected. According to Tromp, the main direction of shear is N–S with conjugate structures in N-W and S-E directions as will be seen in a general map of the region. J. W. Gregory also pointed out that the rifts have developed along the meridian where the

southward moving Zagros-Taurus segment meets the northward moving Alpine segment. In a recent paper (*Proc. Geol. Soc.*, London, 1960, No. 1579, p. 79) Quennel states that the rift valleys have resulted from the doming up of East Africa and subsequent fracture and that they are definitely tensional features.

The Carlsberg Ridge being a part of the major Mid-Ocean system should be expected to be of the same character as the Mid-Atlantic ridge. The latter has a broad base, several hundred kilometres wide and is composed of parallel ridges which gradually rise towards the middle. Along the crest of this zone is a longitudinal cleft 20–30 km. wide and 2–5 km. deep containing basic or ultrabasic igneous rocks at the bottom. The sides of the ridge system appear to be composed largely of basic rocks for the dredgings from these ridges have yielded basalts and related igneous rocks.

It is likely that the ridge system may include a small amount of Sialic material at the junction zone of separated continents at the time of their drifting from each other. Prof. Lester King (1958) has expressed the

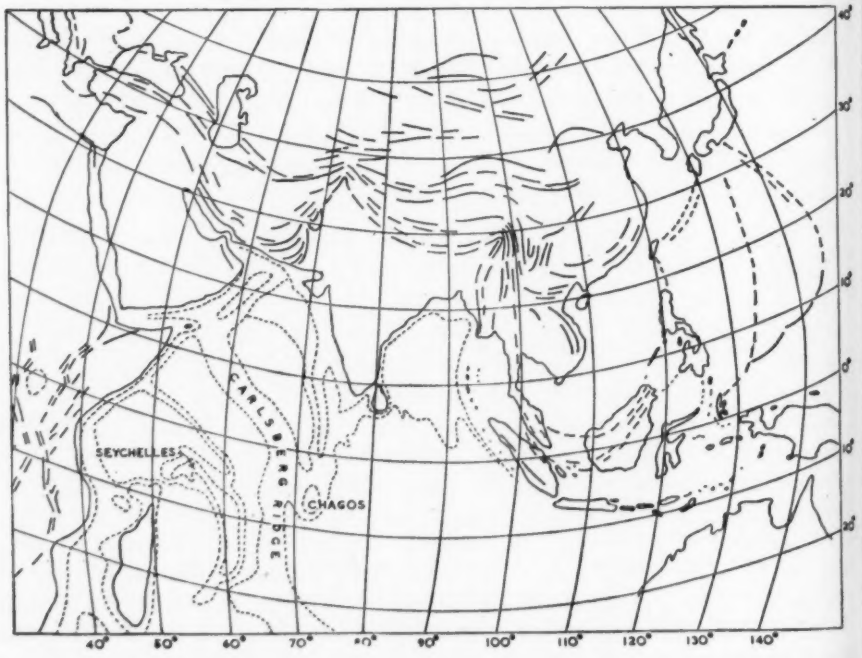

FIG. 3. Southern Asia and the Indian Ocean showing the mountain arcs, mid-Indian ridge and East African rift valleys.

opinion that mid-ocean ridges are of the nature of cicatrices left behind by the separated continents but they appear to be much more, for this would imply only a comparatively narrow rib of Sialic material. It would appear that the subsequent movements of the continents on either side have stretched the crust repeatedly, resulting in the welling up of basic lava along the middle zone and forming the system of parallel ridges. The mid-ocean ridge would, therefore, have been gradually built up by a series of such eruptions, new material coming up in the middle zone after every appreciable movement of the separating land masses.

A single symmetrical ridge system may be formed when the drift is steadily in one direction without any rotation. In the case of India, whose present position has been attained by a translatory as well as rotatory motion, —the motion being in a north-east direction and the rotation in a counter-clockwise direction through about 60°—subsidiary features have also been developed. These features are the Seychelles-Sayade Malha-Reunion ridge and a minor ridge concentric to and north-east of it. The Seychelles ridge though containing some granitic material in the Seychelles, is known to be formed of volcanic islands capped by recent coral growth while the Carlsberg ridge, so far as known, is made up largely of basic igneous rocks. Such an explanation would appear to make a pattern consistent with the idea of the north-eastward drift of India.

The Persian Gulf is a recent feature which originated in the Pliocene and is continuous with the Makran coast fault, along which the original southward extension of Makran has been faulted down in the sea. This faulted area shows a series of parallel ridges and valleys which are the (under-water) continuation of the ridges seen on land. The Oman Mountains are overthrust against the Arabian foreland while the Zagros Mountains which are continuous with them are thrust in a south-west direction over another part of the same foreland. The Persian Gulf is a fore-deep or a furrow formed in front of the Zagros Mountains and is similar to the Indo-Gangetic fore-deep and the ocean deeps in front of the island arcs, there being of course a difference in magnitude between the fore-deep and the ocean deeps. The Persian Gulf bears the same relationship to the Zagros Mountains as the Ganges–Brahmaputra valley does to the Himalayas and both have been filled up during the Pliocene and Pleistocene by sediments derived mainly from the mountain side.

We may digress for a moment to consider the probability of the existence of oil-bearing structures in the folded belt and its neighbourhood. The Himalayan belt represents a marine basin compressed into a small width

marked by numerous high ridges separated by a number of thrust faults. In comparison, the Zagros mountains have probably suffered only a third or fourth of that compression and shortening. Hence, the existence of oil-bearing structures of any appreciable dimensions in the Himalayas is unlikely. The fore-deep may contain some structures, as this belt appears to be less disturbed. There is nothing in India corresponding to the broad foreland of Saudi Arabia with gently folded Mesozoic strata containing some of the richest oil deposits of the world. The southern side of the Gangetic plains which extend towards the Vindhyan uplands may contain some oil fields, but not of the sizes comparable to Saudi Arabian fields.

Finally we come to Central Asia where there is a large thickening of the siatic crust. That this is very abnormal is indicated by the fact that the axes of all the major mountain ranges traversing it are seismically active. Large earthquakes occur also along the Tien Shan and Tannu Ola mountains up to Lake Baikal in Southern Siberia and this may probably connect with the Verkhoyansk Range at one end of which the mid-Atlantic ridge terminates near the mouths of the Lena. As the great gravity anomalies indicate, Central Asia is in a state of disequilibrium which needs readjustment. Such adjustment is in fact taking place along the eastern borders of Asia. As a result of the movement of sialic material from under Asia towards the Pacific (whatever the exact nature of the mechanism) we have a series of island arcs forming along the eastern end south-eastern coasts of Asia. These arcs are of different ages, from the Palæozoic onwards. The outermost arcs of Marianas and Palau islands are being formed at the present day. The Sunda arc constituting the western part of the Indonesian Archipelago has an outer line of small emergent islands which are similarly very young. The main parts of the Japanese, Philippine and the Sunda arcs are of older age, having been raised up in one or two stages before the Tertiary era. The mountain belts on the continental margins as well as these older arcs have experienced the effects of every pulse of compression and uplift over a long period of geological time. And these movements will continue until the Central Asian mass attains equilibrium which is itself affected by the movement of the continental masses.

It will, therefore, be seen that the tectonic features of India and the immediately surrounding areas all fall into a consistent pattern. The drift of India in a north-easterly direction is accompanied by the stretching of the crust in the Indian Ocean which has resulted in formation of the Seychelles ridge, the Red Sea–Carlsberg ridge and the minor ridge between the two. The Tethys basin which existed as an open ocean to the south of Eurasia in the Mesozoic has been converted into a series of mountain ranges by the

movement of and actual impact between Central Asia and India, the original shape of the Indian shield being reflected by the festoons on its northern borders. The result of the drift of India and Australia is the encroachment of continents on to the Pacific by the formation of a series of imbricate mountains and island arcs. These various manifestations are all parts of a single scheme of crustal movement the ultimate cause and mode of operation of which are obscure at present.

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GRANITE TECTONICS OF HYDERABAD*

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1. Introduction

The properties of granite have been a subject of study during the past few years by the author. Physical properties of granites have been studied in great detail and they have been correlated with certain observed geological features. Detailed investigations were also carried out on the deformation of these rocks. The regional data on granites are lacking, as very little work was done on the rock types of this area in the past. In an attempt to fill this void, work was started by the author and is being pursued on these rock types, in order to connect this up with the more extensively studied granites and gneisses of Mysore. For the present, the scope of this work is limited to a small area of about one hundred sq. miles around Hyderabad City. The field data on the structures have been supplemented by the petrofabric studies in the laboratory in order to fully appreciate the deformation suffered by these rocks. The elastic properties of these old rocks (Archæans) are compared with those of less deformed younger granites (Tertiary) of other places in order to study the effect of deformation on the velocity values of sonic waves.

2. Geology of the Area

The area studied is that included in the Secunderabad-Bolarum map (3″ = 1 mile) published by the Survey of India (between Latitudes 17° 24′ and 17° 32½′ and Longitudes 78° 26½′ and 78° 35′), comprising about one hundred sq. miles. This area was chosen because of the availability of such a large-scale map. The terrain forms a part of an undulating granite country. As Mahadevan (1945) has pointed out " the general flatness of the area is relieved here and thereby tors and domes and groups of rocky mountains carved by weathering and mural jointing into fantastic piles of gigantic boulders often having a seemingly unstable and precarious position ". The drainage pattern is dendritic—characteristic of granitic country. The generally accepted stratigraphic sequence (Pascoe, 1950) of the pre-cambrian rocks of this region is as follows:—

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Eparchæan Interval

Quartz Porphyry and Felsite Dykes.

Closepet (Bellary) and other Granites.

Charnockite Suite.

Hornblende and Pyroxene-Granulite Dykes.

Peninsular Gneiss Suite (Gneissose Granites and Gneisses).

Champion Gneisses.

Dharwar System.

In this area, only the Peninsular Gneiss suite with the associated younger dykes are represented, while exposures of Dharwars and Charnockites are not known.

The Peninsular Gneiss suite could be broadly divided into Pink and Grey series of granitic rocks. These are cut by numerous dolerite dykes and veins of aplite, pegmatite and quartz.

Pink Series.—These consist of coarse to fine-grained granites. The colour varies from red to light pink. Porphyritic varieties also are found with large phenocrysts of potash feldspar. They consist of microcline and/or orthoclase, plagioclase (albite—oligoclase), quartz, biotite, hornblende and accessory epidote, apatite, ores, etc. Microcline phenocrysts attain a size of 3 to 4 cm. in the porphyritic varieties.

Grey Series.—These are largely made up of coarse to fine-grained varieties of varied character. The dominant types are intimate admixtures of medium to fine-grained dark granitic rocks associated with pegmatites and aplites. The grey granites are gneissose and fine-grained at places, while at others they exhibit coarse-grained phase. The mineral assemblage consists of orthoclase and/or microcline, plagioclase (albite to andesine), quartz, hornblende, biotite, pyroxenes and accessory apatite, rutile, epidote and ore minerals. That the pyroxene-bearing granites are similar to the acid charnockites is one of the observations made by Sarma and Raja (1958). Much quartz is present even in the dark varieties of granites.

Enclaves.—Both the Pink and Grey series contain inclusions of dark angular bodies (agmatites) as described by Raja (1959). These enclaves are mostly hornblendic and at places schistose, but they show various stages of homogenization towards a normal pink or grey granite. These inclusions are more abundant in the Grey series than in the Pink. It is with these that the pegmatites and aplites are more associated.

Intrusives.—Dolerite dykes with rough E.-W. trend traverse the area from one end to the other. Quartz veins with a N.E.-S.W. trend occur as elongate hillocks. Veinlets of quartz and epidote are quite common. In the pegmatite, graphic intergrowth between quartz and feldspar is clearly seen at places.

The distribution of the above rock types in the area along with structure is shown in Fig. 1.

3. Structure of the Area

Broadly speaking the structural trends of this region seem to conform with those of the Southern Archæan rocks.

Lineation and Foliation.—The general trend of foliation and lineation is North to N.N.W. These structures are more prominent in the Grey series than in the Pink. The streaks and schlieren of ferromagnesium minerals define the foliation planes. The lineation is due to elongated or spindle-shaped clots of hornblende and biotite and parallel to the foliation direction. The foliation is not always apparent but can be seen with careful observation. In a few places these planes are well defined so as to mark the strike and dip. As a matter of fact what appears as traces of folia on the top surface of outcrop is seen to be lost in a regular pattern below the surface. Therefore it has been possible only to mark the trace of the plane. Lineation too has been marked in a similar way, though in general it seems to pitch towards north at a slight angle. A glance at the sketch map will show the general trend to be North to N.N.W., as already mentioned. But at places these trends swing N.E., and even more towards East. Locally, and in particular on smaller outcrops, the trend can no longer be made out among the contorted and confused directions.

The structural map suggests a series of folded rocks whose synclinal folds appear to contain the rocks of the Grey series while the anticlinal portion is occupied by the Pink series. The Grey series is probably the latest phase of the old Dharwar group while the Pink series represent the homogenised or more specifically, granitised phase of the country rocks.

Fracture Pattern.—The granitic rocks of this area show well-developed sets of joints which have been made use of in quarrying. These joints are fracture planes with little or no movement parallel to the plane. Some of the joints have provided room for later intrusions and hydrothermal activity, resulting in dykes and the formation of characteristic minerals of jointing. Good exposures in the vicinity of the city and large-scale quarrying activity have made a detailed joint pattern study possible. Joints could be roughly

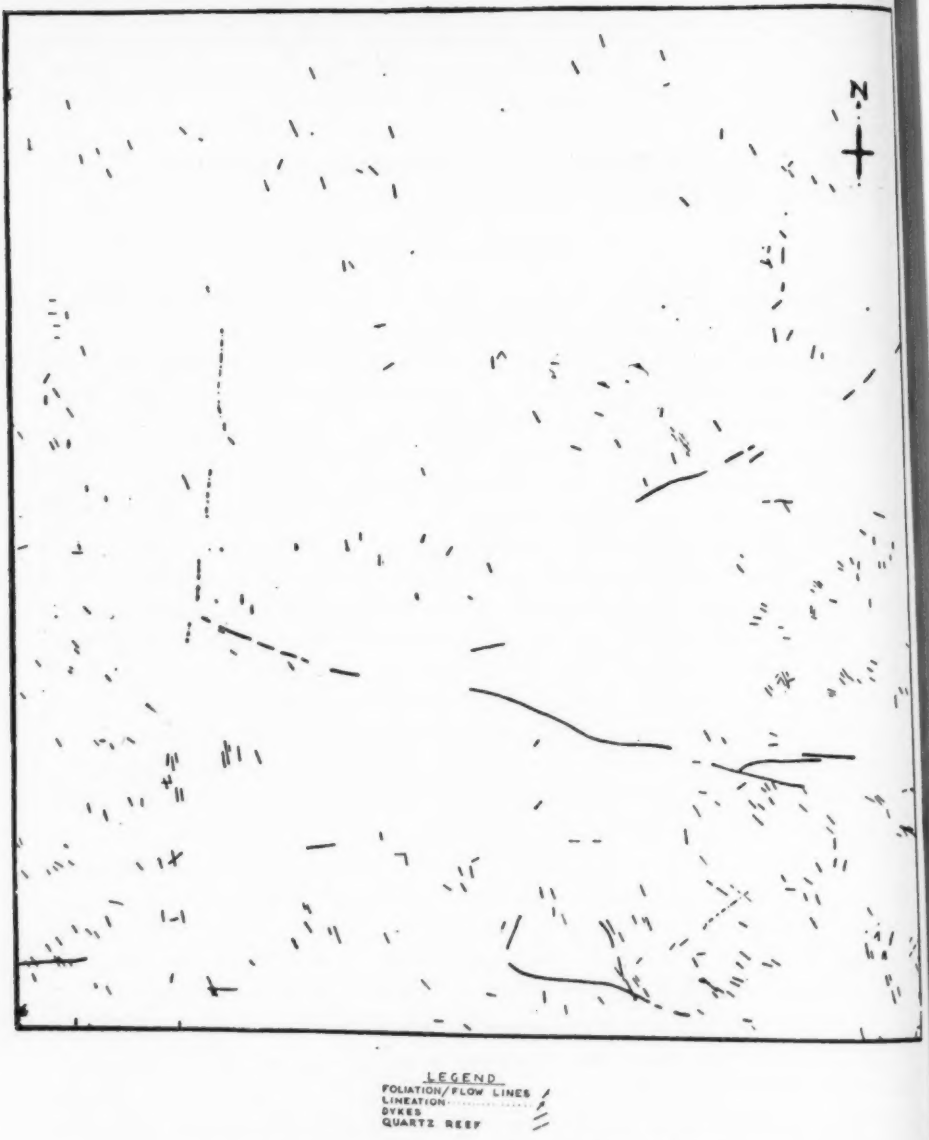

FIG. 1. Tectonic map of Hyderabad (Secunderabad-Bolarum Area).

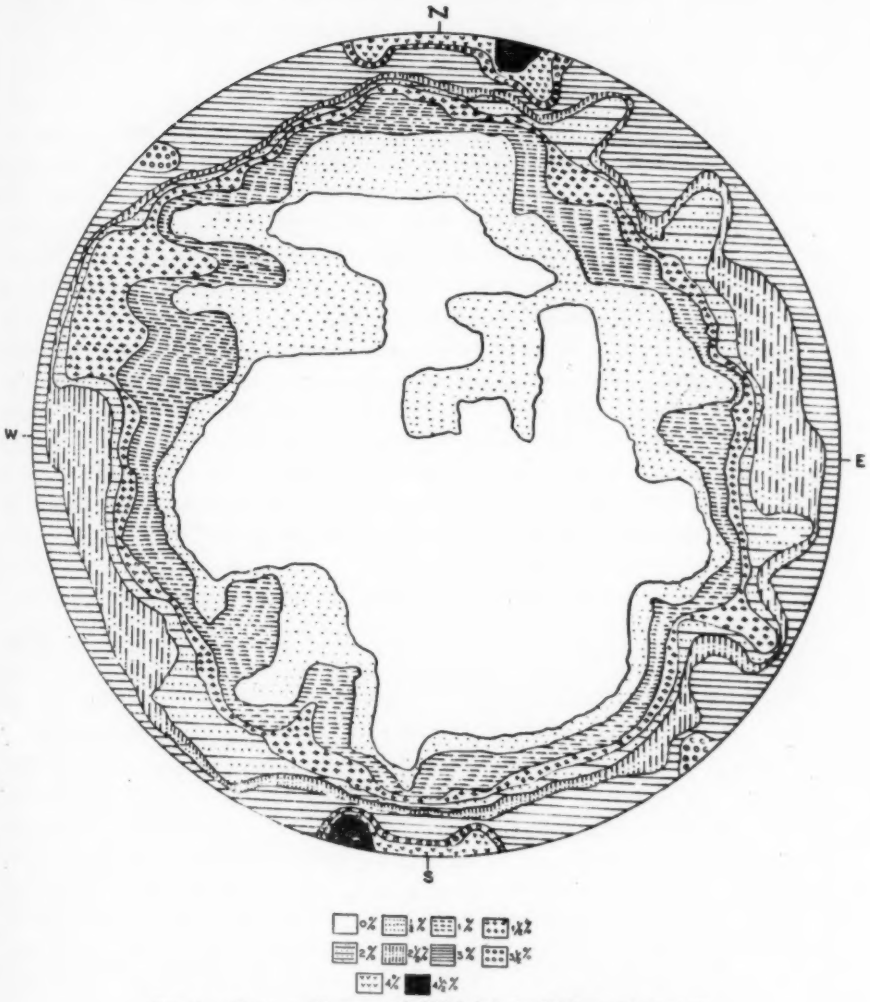

FIG. 2. Contour diagram of 400 joints in Hyderabad granites.

classified into major and minor joints depending on the dominance of fracture in one or more directions. On the other hand, if these are related to the foliation and lineation directions they could be classified according to Cloos (1946) as longitudinal, transverse and diagonal joints depending on whether the joints are parallel, perpendicular or oblique to the lineation direction. The latter classification is based on the mode of emplacement of the granites

by a magma. As these rocks are very ancient and have undergone a number of successive deformations, it is difficult to say whether the joints have any relation at all to the genesis of these granites. Hence they are just described as major and minor joints.

The major joints as seen from Fig. 2 trend roughly E.-W., while the two sets (minor) trend mostly N.-S. varying to N.E. or N.W. The dips as seen from Fig. 2 are rather high and mostly vertical. In quarries the horizontal joints are seen to follow the contours of the surface. The joints are at places closely spaced suggesting zones of intense tension or shearing. The shear zones are characterised by the usual stress mineral epidote and chlorite which forms dark coating on joint planes and veins and stringers in the granite. Faulting on a small scale is also occasionally noticed, the fault plane showing the shear zone development of pyrite along the slickensides. Sometimes faulting is shown by displacement of quartz veins or an inclusion. It is interesting to note that the dolertie dykes follow the major joint direction while veins of reef quartz follow the minor joint direction (N.W.-S.E.). It is also seen that the minor joints apparently continue in the dykes indicating that they are found after the major joints.

4. DEFORMATION IN GRANITES

Structural petrology is concerned with all textural and structural features of rocks; and also with the interpretation of the spatial relations of these textures and structures. The fabric of an object is described by all the spatial data which it contains, irrespective of the exterior shape or boundaries of an object. The spatial relations of fabric elements are grouped together under the general term orientation or preferred orientation in the case of rocks. The orientation obtained may be dimensional in character or it may be of the lattice type or both. Dimensional orientation is expressed by grain shape only with no reference to internal lattice structure, while the lattice orientation describes the internal lattice structure with no reference to the shape of the grains. A study of these orientations is necessary to understand the deformation fabrics.

The specimens for petrofabric study are oriented in the field with respect to structural directions such as lineation and foliation. While dimensional orientation can be best studied in the field, the lattice orientation can only be studied in the laboratory with the usual Universal Stage technique. Thus structural petrology involves systematic study of interrelationship between the structure of rocks in the field and their textures as revealed in the laboratory. Ten specimens (5 pink and 5 grey) of granites have been taken for

fabric study, with their proper orientation marked in the field. Employing the usual Universal Stage technique and plotting the results on the Schmidt equal area net and preparing the fabric diagrams, the lattice deformation has been studied completely. Preferred orientation of quartz grains according to space lattice structure is expressed by the presence of localised areas, called maxima and arcuate zones named girdles, within which the poles of the measured opticaxes are densely concentrated. 100 poles of quartz grains in each granite section cut parallel or perpendicular to strike direction (lineation and foliation) have been plotted in the fabric diagrams.

Deformation in rocks is well understood by considering the symmetry of the fabric and the degree of preferred orientation. In the present investigation of granites, in most cases it can be seen that Peripheral girdles are formed throughout somewhat like concentric circles. Concentration is mostly in the direction of N.N.W.-S.S.E., which incidentally coincides with the strike direction. There are definite maxima in the diagram roughly coinciding with certain important directions. It is quite evident from the petrofabric diagrams that 7 to 12% of the grains are preferentially oriented in all the granites. This indicates that the rocks have undergone a high degree of deformation. The study of fabric diagrams indicate a movement along the plane of gneissosity, with stress acting perpendicular to it.

This dimensional orientation and lattice orientation, commonly understood as rock deformation, has been found to have considerable influence on elasticity of rocks and this will be discussed presently.

5. Elasticity of Granites

The author has been engaged for past few years in studying the physical properties of rocks and correlating them to certain important geological features. Several measurements of ultrasonic velocities, both longitudinal (V_L) and torsional (V_T), have been made at atmospheric pressure and at high pressures on almost all types of Indian rocks, employing different techniques. It has been observed that longitudinal velocities range from 5·6 to 7·5 km./sec. while the torsional velocities are in the range of 2·8 to 3·8 km./sec. One important result of these investigations which stands out prominently is that the granites of Peninsular India exhibit a high velocity value even at atmospheric pressure and room temperature when compared to similar rock types from other countries. In granitic rocks, sound is absorbed probably due to scattering and consequently the attenuation is found to be very high. For these and other reasons it was thought desirable to make a detailed study of elasticity of granites with special reference to measurement

of ultrasonic velocities and the transmission of sound. The dependence of the transmission of ultrasonics on particle size and texture and the velocity values on high pressures, dimensional orientation and lattice orientation (rock deformation) will be discussed.

Employing the phenomenon of total internal reflection of a sound wave at liquid-solid interface, a technique has been developed for measuring Ultrasonic Velocities in solids using pulsed Ultrasonic beams by Krishna Murthy and Balakrishna (1952). With the help of the above method a number of measurements have been made on Hyderabad granites. The velocity values, both V_L and V_T in km./sec. at ordinary conditions in number of granites are given in Table I.

TABLE I

Ultrasonic velocities in Hyderabad granites

Sl. No.	Density gm./c.c.	V_L	V_T
1	2·68	6·40	3·41
2	2·68	6·15	3·2
3	2·65	5·32	3·0
4	3·69	6·37	3·3
5	2·70	6·90	3·0
6	2·68	6·40	2·9
7	2·70	6·90	3·5
8	2·67	6·21	2·6
9	2·68	6·13	2·6
10	2·67	6·20	3·3

In Table I, it can be clearly seen that the velocities in these granites are around V_L (6·3 km./sec.) and V_T (3·0 km./sec.). These values are found to be higher in comparison with those of some American granites. In Table II are given the values of some Indian granites (by the author) and those of American granites (by Birch) at atmospheric pressure and also at high pressure of the order of 10,000 bars, in km./sec.

TABLE II

Comparison of ultrasonic velocities in Indian and American granites

	Locality	Density gm./c.c.	$V_{p(1\ bar)}$	$V_{p(10,000\ bars)}$
1.	Rockport, U.S.A.	2·62	5·0	6·51
2.	Quincy, U.S.A.	2·62	5·0	6·42
3.	Barre, U.S.A.	2·65	5·1	6·39
4.	Chemsford, U.S.A.	2·63	4·2	6·35
5.	Minnesota, U.S.A.	2·67	6·0	6·48
6.	India	2·66	6·15	6·66
7.	India	2·65	6·32	6·68
8.	India	2·74	6·00	6·39

6. ROCK DEFORMATION AND ELASTICITY

In this section an attempt is made to discuss the relationship between rock deformation and elasticity of rocks.

The orientation of quartz grains in granites which is a result of rock deformation, as studied by Universal Stage, has been discussed in detail in Section 4. It has been concluded there that these granites have been deformed, having been subjected to stresses in the crust.

When compared with the values in Table I, the results in Table II suggest that the Hyderabad granites which are older (Archæan) have been more deformed than in American granites which are younger (Tertiary). Further, though the velocity values in both the types of granites differ at atmospheric pressure, they tend to reach almost the same values at higher pressure (10,000 bars). It is interesting to note the behaviour of the values in the two types of granites as pressure increases. Figure 3 shows peculiar behaviour.

An examination of the graph suggests that American granites (A) which are younger and consequently less deformed show a steeper rise in the beginning (*i.e.*, value increases rapidly as pore spaces close up) and later attains

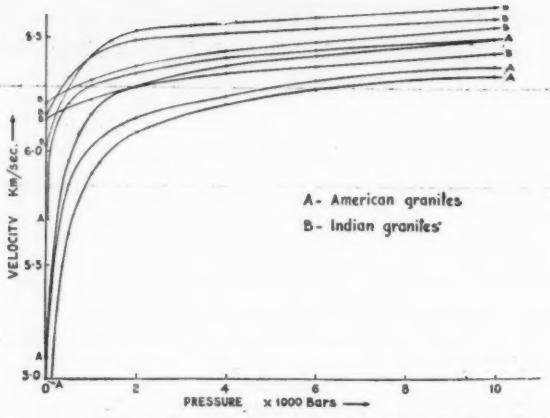

FIG. 3. Variation of Ultrasonic Velocities with pressure.

a steady value. This dependence of the velocity value on the deformation history of a rock is interesting.

Another interesting feature observed during this investigation is that as a higher degree of preferred orientation sets in a specimen, a higher degree of anisotropy is exhibited. This is understandable because rocks, which are in the nature of polycrystalline aggregates, where the crystallites are randomly oriented, are found to be elastically isotropic.

Dimensional orientation, which is a direct consequence of the movements that have taken place, is expressed by the presence of lineation and foliation. The author (1959) has studied the effect of dimensional orientation on ultrasonic velocities in rocks, and discussed the results in detail. The data on granitic rocks of Hyderabad are presented in Table III. Velocities were measured in plates cut perpendicular to definite reference directions, namely, foliation and lineation. One section is cut parallel to the reference direction and velocities are measured in a direction perpendicular to lineation (*a*), while the other is cut perpendicular to reference direction and velocities are measured in a direction parallel to lineation (*b*).

It is seen from Table III that the velocity values in the direction (*a*), are consistently higher than in the direction (*b*) in all the cases. This is to be expected because more compaction has taken place in the direction perpendicular to the lineation because of the stresses which had acted on the rocks. Similar variation is noted in both the velocity values (V_L and V_T)

TABLE III

Velocities in dimensionally oriented granites

Sl. No.	*a*		*b*	
	V_L	V_T	V_L	V_T
1	6·9	2·5	6·3	2·4
2	6·9	2·4	6·2	2·3
3	6·4	3·0	6·2	2·9
4	6·2	2·9	6·0	2·8
5	6·1	2·9	5·7	2·6
6	6·1	3·1	5·5	2·7
7	6·3	3·0	5·8	2·6
8	6.7	3.2	6.2	2.7

in all the cases. This is in conformity with the earlier observation of the author (1959).

7. CONCLUSION

Pink and Grey types of granites are found in and around Hyderabad City, although definite boundaries could not be always drawn in the field. Minor faults and numerous dykes are noticed in the area. The fracture pattern indicates that major joints follow the lineation direction. Petrofabric studies of these granites suggest that they have been appreciably deformed. Ultrasonic Velocities have been measured in a number of granites and it was found that values are around $V_L = 6·3$ km./sec. and $V_T = 3·0$ km./sec. Dimensional orientation and lattice orientation has a considerable influence on velocity values in granites. It has been observed that velocity value is higher in a direction perpendicular to lineation than in one parallel to it.

It is a pleasure to acknowledge the help given by Mr. N. Raja, in preparing this manuscript and in particular the sketch map showing the distribution of rock types and the structure.

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OROGENESIS MAGMAS AND METAMORPHISM*

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Abstract

Tectonism, volcanism, plutonism and metamorphism are interdependent and contribute to the fabric of orogens and igneous rocks therein. Major lines of thought on problems relating to orogenesis in relation to igneous and metamorphic activity, generation of magma, rise of magma, and polymorphism and isostasy in crustal deformation, are outlined. The mechanics of emplacement of magma, at higher crustal levels, and the resultant fabric patterns are discussed at some length, as they are pertinent in interpretation of field data. The emplacement of granites and the major ideas in the generation of granite magma are discussed, and the new concepts of Buddington on the nature of emplacement of granite bodies, found at various crustal levels, presented. The tectonic implication of peridotites and serpentines, and the controversy over their mechanism of emplacement, are reviewed briefly. The concept of Hess that serpentinization below the Mohorovicic results in volume changes actuating mechanical movements such as uplifts, is suggested as applicable to the mechanics of uplift of sections of the stable Peninsular block of India.

Neither Volcanism nor Plutonism can be understood until we understand the formation of Maintain Chains.

—R. A. Daly, 1925.

Introduction

The close relationship of igneous action to crustal deformation is exemplified by the prevalence of active volcanos along the major seismic belts of the earth's crust. Orogens are characterised by intense magmatic activity, as evidenced by chains of granite and granodiorite **Batholiths**, and belts of **Ultramafites**. Similarly, the basement rocks in tectonic belts carry the impress of several cycles of metamorphism of varied character. The problem of deciphering the precise relationship between **Tectonism**, **Volcanism**, **Plutonism** and **Metamorphism** is not simple, and requires careful analysis

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of a wealth of structural, stratigraphic, geochronological, petrographic and geochemical data. An attempt will be made here to outline some major lines of thought, and present some data of significance to field geologists.

GENERATION OF MAGMA

Crustal movements condition the generation of magmas and their passage to higher levels. Potential magma layers of the crust, when downfolded and pushed to deeper levels where the temperature is above their melting point, melt and generate liquid magma. Similarly, arching movements of the type proposed by Yoder result in crustal layers moving up to higher levels, and suffering sudden relief of pressure, resulting in their partial melting and generation of magma. The generation of parent magmas by tectonism conditioning the melting of appropriate crustal layers of the earth, has been envisaged by Stille, Buddington, Wahl and others.

MAGMA CYCLES

The cycle of magmatic activity in OROGENS differs in accordance with their antiquity. Younger orogens are characterised by (*i*) A geosynclinal phase with intrusion of BASIC and ULTRAMAFIC types (Ophiolites), and extrusion of SPILITIC lavas; (*ii*) A syntectonic phase with emplacement of GRANITE magma and intense migmatization, followed by late tectonic emplacement of GRANITIC and GRANODIORITIC batholiths; (*iii*) A post-tectonic volcanic eruptive phase with extrusion of ANDESITIC lavas and (*iv*) An eruptive phase with extrusion and injection of BASALTIC magma after which the region ceases to be a mobile belt. In older orogens of the Archæan, a different pattern is envisaged, as exemplified in the Fennoscandian shield, where a zone of PRIMOROGENITIC granites with extensive granitization and BASIC and ULTRAMAFIC volcanic action, is followed by a zone of serorogenic granites, actuating migmatization and granitization, with a final phase marked by emplacement of post-orogenic granites.

PARENTAL MAGMAS

During orogenesis, the generation of four primary parental magmas envisaged by Wahl (1949), (1) SPILITIC magma grading to a PICRITIC types, (2) GRANODIORITIC magma which will differentiate to a variety of rock, varying from GRANITES to PERIDOTITES, (3) BASALTIC magma and (4) POTASH GRANITE magma (granite eutectic composition). When crustal movements attain a cratogenic character THOLEIITIC and OLIVINE-BASALTIC magmas are generated the former from the upper Simatic layer and the latter from greater depths, while granitic magma differentiates into POTASH GRANITE and GABBRO-ANORTHOSITE-NORITE. CHARNOCKITIC magmas differentiating

into granitic, syenitic and granodioritic variants as suggested by the writer (Subramaniam, 1959) and FOYAITIC magmas differentiating into a variety of alkalic sub-magmas, may also be cratogenic in character. PERIDOTITIC and PYROXENITIC magmas may also be generated by fusion of the lowest part of the simatic shell under cratogenic conditions.

Buddington (1943) has visualised a primordial layering of the basaltic layer of the upper crust, simulating it to that obtaining in density stratified sheets like the Bushveld, Stillwater and Skaergaard. According to his diagrammatic representation, deformation of the crustal layers will have essentially the effect of displacing the fusion curves for each rock layer with respect to the Temperature-Depth curve. When the temperature-depth curve is raised relative to and lies above the fusion curve for the respective kind of rock, the appropriate magma will be formed. While gabbroic magma would be dominant and recurrent as it can form throughout a wide environmental range, peridotite magma will be generated only under exceptional structural dynamics. Buddington has envisaged the generation of a gabbroic anorthosite magma by partial melting of the Bytownite-Anorthosite layer. The position of this crustal layer as envisaged is such that its melting can take place only under exceptional conditions. The exclusive occurrence of large masses of intrusive anorthosite, in the Pre-Cambrian, and the rarity of an extrusive equivalent of this type of anorthosite, are in conformity with the hypothesis.

POLYMORPHISM AND ISOSTASY

In 1937, Bernal and Jeffrys suggested that polymorphic rearrangement of the crystal structure of OLIVINE $(MgFe)_2 SiO_4$ might explain certain discontinuities within the mantle. Mason (1953) proposed that an increase in the amount of a denser polymorph could lead to the contraction of the earth resulting in crustal shortening and orogeny. It is suggested that polymorphic transitions take place along a fairly wide zone, as the rates of transformation vary with depth, temperature and pressure. The volume changes resulting from polymorphic transitions will produce a purely mechanical effect, the increased pressure due to such volume changes resulting in fracturing of the crust. Relative motion of molecules during polymorphic transitions may also dissipate shear stresses. Polymorphic transitions with consequent volume changes may be a significant factor in Isostatic adjustments, which in turn induce geochemical changes actuating melting of crustal layers. Similarly, geochemical phase transformations at sub-crustal levels result in large volume changes, which may induce epeirogenic movements and uplifts. Hess (1955) has speculated on volume changes consequent

on serpentinization of olivine rock below the Mohorovicic, to account for epeirogenic movements of the sea floor, and the uplift of the Colorado plateau. It is not inconceivable that a similar mechanism may have been operative in the upiift of certain sections of the stable peninsular block of India.

MECHANICS OF EMPLACEMENT OF IGNEOUS ROCKS

Emplacements of magma at higher crustal levels involves a variety of processes dependent on the nature of the magmatic source, time of emplacement, and crustal tectonics. These are classified as below (following Professor Buddington's lectures)*:

Mechanism	*Mechanics*	*Fabrics*
1. *Quiescent Emplacement:*		
(*a*) *Stoping*—		
(i) Piecemeal stoping	(i) Magma is generally less dense than country rock and therefore tends to rise along joints, fractures, etc.	(i) Batholiths (?)
(ii) Ring fracture stoping.	(ii) Blocks of country rock work free and sink into magma chamber. In a few instances country rock is lighter than magma—*e.g.*, blocks stoped from the base of diabase sheets and rise upward.	(ii) Blocks of country rock surrounded by fractures sink into magma chamber; sometimes they are moved up.
(iii) Major stoping	(iii) Large blocks of basement rock pushed up by rising magma and absorbed in the magma chamber.	(iii) Batholiths (?) with large blocks of crustal material broken apart by orogeny.
(*b*) *Entry of magma into pre-existing spaces*—		
(i) Tensional fractures	(i) Tensional fractures in plateau volcanic regions lavas are erupted from fissure which are probably of tensional origin.	(i) Fissure lava eruptions and island are volcanics.
(ii) Pore space	(ii) The origin of the fissures is not completely understood but it would seem that they penetrate to the depth of the "basalt layer" and thus permit the rise of basaltic magma.	(ii) Magma or magmatic vapours permeate pore space.

* Graduate Course Lectures on Structural Petrology given at the Princeton University.

Mechanism	*Mechanics*	*Fabrics*
(iii) Subcrustal space	(iii) Rise in response to differential pressure.	(iii) Doubtful.
(*c*) *Subsidence with consequent rise of magma—*		
(i) Cauldron subsidence	(i) Involves development of ring-type fractures and settling of crustal blocks into magma chamber. May be subaerial or sub-terranean.	(i) Cauldrons, ring dykes and cone sheets.
(ii) Floor subsidence	(ii) Involves sinking of the floor of intrusive masses into large magma chamber below.	(ii) Lopoliths and ethmoliths
II. *Forceful Injection:*		
(*a*) *By moving overlying rock—* (1) Upthrusting (2) Doming (3) Lifting	(1–3) Pressure of magma forces rock upward. Therefore characteristic of shallow depth —hypabyssal range.	(i–iii) Sills with flat dips; flat lying sheets; Laccoliths, Bysmaliths. Cone sheets with vertical displacement, stocks, Batholiths (of shallow depth), and Feeders to layered bodies.
(*b*) *By thrusting country rock aside*	Wall rock thrust laterally by force of magma. Believed characteristic of intrusion at depth and found in association with larger intrusive masses.	Batholiths with marginal thrusts and peripheral foliation.
(*c*) *By combinations of* a *and* b.	..	Laccoliths and some ring dykes and cone sheets.
(*d*) *By thrusting country rock downward*	Emplacement by downward thrusting of roof.	Ethmoliths.
(*e*) *Displacement direction doubtful*	Passive emplacement in space created by crustal movements induced.	Where displacement direction is not definitely known the form may be a Phacolith or Harpolith.
III. *Diapiric:*	Analogous to the emplacement of salt domes—strata are thrust outward and upward to allow emplacement. This is perhaps most characteristic of orogens.	Large tear-shaped intrusives which may have roots.

Mechanism	*Mechanics*	*Fabrics*
IV. *Chemical emplacement:*		Batholithic massifs
(*a*) *Regional melting at depth*		
(1) Magma generated and crystallizes in same place	Involves heating of sialic material and consequent generation of magma. This may be accomplished by down-buckling of the crust so that it is brought into a zone of high temperature. Possibly the granitic rocks of orogenic regions are developed in the sialic material which is depressed in a tectogene.	
(2) Magma generated and moves to higher level prior to crystallization	The palingenetic magma may either crystallize *in situ* or may be intruded into overlying rocks. If it is intruded, then the mechanics involved may be diapiric.	
(*b*) *Local melting in the upper crust by heat of invading magma*	This concept involves superheat in the invading magma. Not important as far as emplacement is concerned.	
(*c*) *Melting through the action of volcanic gas*	Of little importance in large-scale emplacement.	
(*d*) *Replacement through the action of granitizing liquids or gases*	Involves the concept of transforming solid rocks to rocks of granitic character, without passing through a magmatic stage. Several mechanisms postulated, but none have been substantiated.	

In summary it may be said that one or more of the following processes may have been important in the emplacement of a given igneous mass:

(i) Quiescent upward motion of magma.

(ii) Forceful injection of magma.

(iii) Diapiric injection of magma.

(iv) Replacement.

The forces impelling the magma for each of the first three processes must necessarily have varied. Presumably, the difference in specific gravity between magma and country rock is sufficient to permit quiescent emplacement by stoping, cauldron subsidence, etc. Forceful injection, however, requires additional impelling force. The nature of this additional force is not known but most investigators believe it to be consequent upon orogeny, magma being forced upward by lateral stresses. Diapiric injection probably involves a combination of both.

Several fabric patterns serve to distinguish the mechanics involved in the emplacement of igneous rocks. The most diagnostic are those characteristic of forceful injection. These are listed below:

(*a*) External fabrics indicative of magmatic pressure:

(i) Outflow of magma at a high elevation.

(ii) Upward motion of inclusions.

(iii) Uplift of roof rocks—folding, jointing, faulting.

(iv) Updrag of bedding, fold axes, linear structures, etc.

(v) Peripheral folds.

(vi) Peripheral foliation planes.

(vii) Faults.

(viii) Border mylonites.

(*b*) Internal fabrics indicative of forceful injection:

(i) Linear and planar flow structures.

(ii) Orientation of inclusions, segregations, etc.

(iii) Primary fracture systems—cross joints, longitudinal joints, diagonal joints, primary flats joints.

(iv) Flexures in flow layers.

(v) Marginal thrusts.

Fabrics of the above type are not observed in masses emplaced by stoping; some, however, may be present in intrusives emplaced through diapiric mechanics.

Rise of Magma

Movement of magma is dependent on several factors and the mechanics of intrusion of thin fluid magma differs from the mechanics of intrusion of viscous magmas.

Causes of magma motion:

(1) Gravitative adjustment—Modification of density by vesiculation, partial crystallization or changes of temperature (Passive).

(2) Lateral thrusts—Crustal movements and magma movements are co-ordinate but neither can be demonstrated being cause of the other (Aggressive).

Extrusion is also controlled by crustal tectonics. Fissure eruptions are characteristic of region which have suffered vertical crustal movements where lateral movements are only consequential, while central type of eruption is characteristic of areas which have suffered lateral movements of the Alpine type.

EMPLACEMENT OF GRANITE

According to Wahl (1949) isostatic adjustment during orogenic down-buckling results in the partial fusion of feldspathic components of the rocks. The molten feldspars will naturally carry quartz, water vapour, and small amounts of mafic material in solution and thus approximate in composition, an ideal granite. The generation of granitic liquid has been discussed at great length by Wahl (1936, 1943), Sederholm (1933), Bowen (1928), Eskola (1932, 1933, 1936, 1955) Holmes (1932), Stille (1939), Buddington (1943), Paige (1955), Reed (1955), Gorai (1960) and others. The major processes envisaged are:

(1) By fusion of geosynclinal sediments (Palingenesis).

(2) By refusion of the base of the granitic layer of the earth (Protectite).

(3) By differentiation of a syntectic magma formed by the solution of granites or other salic material in basaltic magma (migma + magma).

(4) Differentiation of basaltic magma as such (True magma).

(5) Through partial refusion of the upper mantle under relatively high pressure condition.

In recent times, the older French and Fennoscandian schools of thought on the origin of large granite massifs by a process of granitization has been ably advocated by Reed (1955, 1957) in a series of addresses. He has proposed a GRANITE SERIES, correlating time and crustal level, with formation of granitic rocks in an orogenic belt. Recently, Buddington (1959) has critically reviewed the existing tectonic data, particularly on North American Granites, and offered a major revision to Reed's concepts. Buddington has evaluated the emplacement mechanism on the basis of the external and internal structures of granite bodies found at different crustal levels, or rather at physical conditions obtaining at such crustal levels. He has suggested the terms CATAZONAL, MESOZONAL and EPIZONAL to granites formed at temperature depth-zones obtaining at depths of 7–12 miles, 5–9 miles and

0-4 miles. Buddington has pointed out that granites of the epizone are wholly discordant, those of the mesozone partly concordant and partly discordant, and those of the catazone predominantly concordant. Granitization is regarded by him as the major process involved in the formation of catazonal granite massifs, subordinate in the formation of granites of the mesozone and minor or local in the formation of epizonal plutons.

Ultramafic Magmas and Tectonism

The tectonic implications of large masses of Peridotites and Serpentines have been discussed by Benson (1926) and Hess (1938, 1939, 1954, 1955). The latter has expounded at length the mechanism of emplacement of such ultramafic bodies, the nature of the primary magma and its source, the types of ultramafic rocks in various tectonic settings, and the relation of large-scale serpentine belts to global deformational features like the Island Arcs. During a study of the gravity anomalies in the West Indian islands arc, Hess noticed the close association of a belt of serpentinized peridotite intrusions with a zone of strong negative anomaly. The anomaly is interpreted to be an intense zone of deformation, representing a major downbuckle, or Tectogene. During its formation, the base of the relatively strong upper crust came into contact with a peridotitic substratum whose upper portions underwent partial fusion and were squeezed off. The relatively rigid and strongly deformed downbuckle allowed the hydrous peridotite magma to migrate upwards and get emplaced either along the axis of the downbuckle or on either side of it.

The nature of the ultramafics during emplacement has been a matter of controversy, the field evidence being opposed to the conclusions based on experimental studies on the system MgO–SiO_2–H_2O. The field geologists conceive of a Peridotite Magma rich in water emplaced in a fluid state, while the experimentalists preclude the possibility of a peridotite magma at such temperatures. Emplacement of Peridotite or Serpentine in the solid state with their mobility facilitating movement along tectonic zones, has been established in certain cases, but this mechanism is not applicable in many other instances. Other lines of field and laboratory evidence strongly favour emplacement of a liquid ultramafic magma.

MacKenzie (1960, pp. 312-13) has discussed the temperature of intrusion of the Tinaquillo peridotite from Venezuela, and based on the structure and composition of garnets and pyroxenes at the contacts, estimated the temperature of intrusion to be between 800° C. and 1,000° C. This problem merits further investigation in the field and laboratory. Reed (1954) regards

serpentines anomalous and has aptly described them as slippery tectonic pods.

Yoder and Tilley (1958–59, pp. 89–94) have experimentally sought elucidation of Fermor's conception of an Infra-plutonic shell of eclogite in the sub-crustal zone. They have regarded that eclogites would be a potential source of basalt. By varied experimentation under appropriate conditions, they have demonstrated that eclogites could be converted to basalt, pyroxenite or hornblendite, and by partial melting of eclogite either of two major types of basalt may be generated.

TECTONISM AND METAMORPHISM

Changed physical conditions induced by crustal deformation such as downfolding to deeper levels and arching or doming to higher levels, will result in mineralogical and textural changes in the rocks of the crust. The metamorphic changes attendant on deformation have been defined in the depth-temperature zonal classification of Becke, Grubennmann and Niggli, and the Facies concept of Eskola. Recent experimental work has revealed that factors other than temperature may lead to the formation of rocks generally thought to have formed in a particular depth-temperature intensity zone. For example, eclogites which are generally regarded as Catazonal and formed under highest pressure conditions, are also found in younger orogens in association with low pressure assemblages. The role of water and other fluids, moving along the intergranular boundaries and acting as a catalyst has been emphasized; the movement of these pore fluids is perhaps controlled by crustal movements. The basement of an orogen does not remain passive during diastrophism, but is rejuvenated, by differential anatexis and introduction of granitizing fluids and ichors, consequently attaining mobility to the extent of initiating intrusion. The mobilised infra structure forces itself up into the super-structure as visualised by Wegmann (1935). High grade metamorphism, granitization and orogeny may therefore be regarded as related events. According to Reed (1954) widespread low grade metamorphism is associated directly with orogeny, followed later by superimposition of granitization metamorphism. He regards permeation of metasomatic solutions to be related to regional metamorphism.

According to Waters (1955) in a crustal downbuckle, of the tectogene type, water and other easily removable constituents move out of the geosynclinal prism and mix up with tholeiite, modifying it to an explosive andesite. Continued metamorphism of the tectogene root results in the emplacement of TRONDJHEMITIC and GRANODIORITIC batholiths. Prolonged anatexis

will leave behind a roof of GREENSTONES, LIMESTONES and SERPENTINES which are transformed by dehydration, actuated by increasing metamorphism, to AMPHIBOLITES, SKARNS, and URALITIZED or BIOTITIZED ULTRAMAFITES. Partial local melting of the rocks will result in the formation of alkalic mafic lavas which are erupted.

SOME PROBLEMS

Except for an excellent summary by Krishnan (1953) little or no attempt has been made in India to decipher the relationship between Tectonism, Igneous activity and Metamorphism. A wide field is open to workers, and the older publications of the Geological Survey contain a wealth of valuable data meriting reinterpretation and analysis.

The Archæan shield area of the Indian Peninsula offers unrivalled scope for studies of precambian tectonics. The Charnockite suite of rocks, and the Alkalic rocks of MADRAS, KERALA, ANDHRA, ORISSA and RAJASTHAN, which are perhaps cratogenic, merit detailed studies, particularly with regard to their tectonic setting. Similarly the Archæan Ultramafics which have undergone metamorphic reconstitution have to be carefully examined and their primary nature established. The granites of India present a variety of complex problems concerning their tectonics, emplacement mechanism, and geochemistry, while the Deccan basalts offer a rare challenge. The mechanism of extrusion of the Deccan basalts is not clear and the presence of flows which can be traced uninterrupted to distances of over 50 miles is a remarkable feature.

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HISTOGENESIS OF THE VENATION PATTERN IN THE LEAVES OF *POLYALTHIA LONGIFOLIA*

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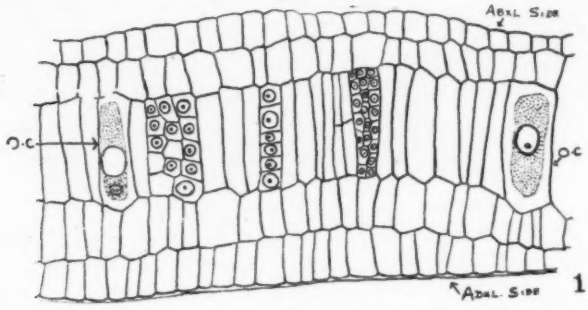
Introduction

This contribution embodies the results of studies on the ontogeny and pattern of venation in the leaves of *Polyalthia longifolia*. The structure of the shoot apex and the initiation of foliar primordia have already been dealt with in an earlier paper (Ramji, 1960). Foster's review (1952) on the topic illustrates the occurrence of considerable range of variation in the development and the adult pattern of vascularisation in the leaves of angiosperms. Subsequent to Foster's review, Pray (1954, 1955 *a b, c*) has reported the development of foliar vasculature in some liliaceous and magnoliaceous members.

Observations

As has been reported earlier (Ramji, 1960), the leaf primordia in *Polyalthia longifolia* arise in an alternate pattern, the initiation of the appendage taking place in the second tunica layer. The apical growth of foliar primordia ceases when they have attaind a length of about 770 microns. The lateral expansion of the lamina is brought about by the activity of the marginal meristem. The sub-marginal-initial cell divides anticlinally giving derivatives to the abaxial and adaxial hypodermal layers of the lamina. The adaxial hypodermal layer, by further divisions, contribute to the middle layer of cells. The constituent cells of this layer elongate considerably in the direction of the thickness of the leaf. The initiation of the procambium takes place in some of these cells (Fig. 1).

The venation pattern of the leaf is pinnate, the secondary veins traversing obliquely from the midrib and anastomosing with adjacent ones by tertiary veins near the margin. The procambium in the petiole and in the costa is differentiated during the apical growth of primordium, whereas the time of origin of this tissue in the veins of other categories is postponed until the formation of the lamina.



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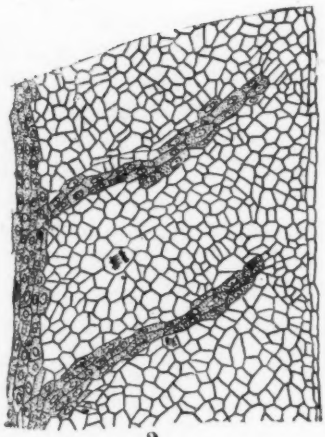

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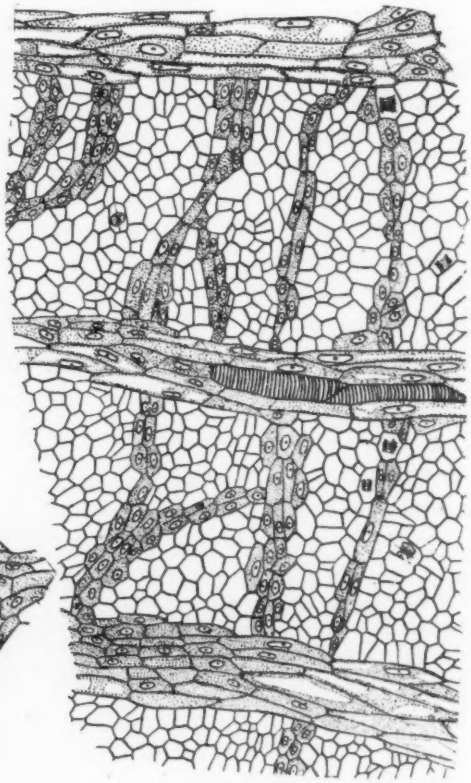

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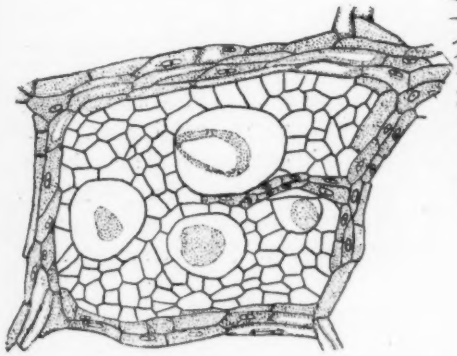

4

TEXT-FIGS. 1-4

Secondary veins.—As mentioned above, the origin of the secondary veins is traceable to the middle layer of cells (Fig. 1). Either isolated cells or small groups of adjacently placed cells of this layer undergo divisions essentially in the periclinal plane and produce short strands of smaller cells, each derivative group consisting of 5–10 cells. Further study of the venation pattern is based on serial paradermal sections at various stages of vein development.

The plate-meristem, prior to the differentiation of procambium, consists of more or less homogeneously appearing cells with no particular alignment (Fig. 5). The secondary veins differentiate in a progressive manner from the procambial midrib, across the lamina, towards the margin of the leaf. In relation to the length of the leaf, the secondary veins differentiate earlier in the basal part, and this wave spreads towards the apex. It should also be stated that the procambial strand of the secondary vein is always in continuation with that of the midrib, and is uninterrupted during its course. As may be seen from Figs. 1 and 2, the procambial cells of this category of veins are in multiseriate arrangement, although occasionally one may come across a biseriate situation. However, the latter condition soon changes over to the multiseriate type generally by the division in the procambial mother cells themselves and occasionally by the differentiation of the adjacently placed cells of the ground tissue which elongate or divide to turn out into procambium. Under the latter condition, the concerned cells which invariably neighbour the procambium assume procambial characteristics and thereby add to the thickness; occasionally, the concerned cells may divide whereby the daughter cells become incorporated into the procambium. With the enlargement of the lamina in surface area due to the activity of the submarginal-initial cell and to the intercalary growth, procambial differentiation also takes place hand in hand so that a larger number of secondary veins is formed. One or two of the procambial cells here and there mature into protoxylem elements while the intervening cells break the continuity. At a later stage, however, the latter kind of cells also matures into similar xylary elements whereby the xylem strand as a whole becomes continuous. Such a discontinuous maturation of the protoxylem is in contrast to the continuous nature of differentiation of the protophloem in the secondaries. While the differentiation of the procambium of the newer secondary vein proceeds nearer the upper half of the lamina, interconnections (*i.e.*, tertiaries) begin to differentiate at the basal half.

Tertiary veins and minor veinlets.—The tertiary veins are initiated in between the secondaries. Prior to the differentiation of the tertiary vein procambium, the plate-meristem consists of isodiametric cells. The tertiaries

are differentiated as uni- or biseriate strips of cells in between the adjacent secondary veins (Fig. 3). The origin of these cells is usually simultaneous. A continuous series of cells that extends from one secondary vein to the adjacent one elongates to assume the shape of procambial cells (Fig. 3). While such a simultaneous nature of differentiation of the tertiary vein was found to be the usual condition, it was not uncommon to observe here and there a progressive type of differentiation. Figure 6 shows the procambial strip that extends from one secondary vein to the other. In this tertiary vein procambium, while a chain of cells has elongated to assume the conventional form of procambial cells, the presence of unelongated meristematic cells at the lower half breaks the continuity (arrow in Fig. 6). Such cells may elongate belatedly so as to establish connection with the adjacent secondary vein procambium (Fig. 3).

The initially uni- or biseriate strips of tertiary vein procambium soon becomes multiseriate primarily due to divisions in the procambial cells themselves. It was not uncommon to observe a cell of the adjoining ground meristem elongating and becoming incorporated in the procambium. Along with the establishment of the tertiary vein procambium, the ground tissue increases in surface area due to intercalary divisions. The tertiary vein procambium keeps pace with this increase. By the time the tertiary veins are established in the leaf, the primary vascular tissues become fully organised in the secondary vein procambium.

Quarternary and minor veins.—The quarternary veins are those that occur in between the tertiaries. Generally uniseriate or occasionally biseriate strips of cells of the ground tissue elongate simultaneously in between tertiaries and become quarternary vein procambial strips. Concomitantly, the procambial tissue of progressively higher orders of the vein system also becomes differentiated. At such a stage, it becomes highly difficult to follow the vein category beyond the tertiary order (Fig. 7). The ground tissue becomes traversed by the procambial system of minor veinlets in such a complicated fashion that the yet undifferentiated portions of the lamina are resolved into numerous areoles. By this time the oil cells also differentiate in the ground tissue. The areoles consist of meristematic cells which are in diverse stages of enlargement and differentiation leading towards the attainment of the mature histological features of the leaf. The areoles are polygonal in outline containing one or two secretory idioblasts (Fig. 7).

The differentiation of the vein endings proceeds progressively. Usually a strip of biseriate cells elongates to become the vein ending (Fig. 4). These ultimate branches are constituted of protoxylem which differentiates

progressively. Vein endings are simple and unbranched and each areo'e contains often two endings, sometimes one and the tips of these generally are in contact with the secretory idio-blasts.

There is a conspicuous gradual reduction in the number of phloem elements in minor veinlets and it is absent in the vein endings. Figure 8 shows the paradermal section of a mature lamina in which full tissue differentiation has occurred. The entire complements of the spongy mesophyll, the veins and prominent intercellular spaces among the mesophyll have all developed. A transection of the leaf at this stage show the two-layered palisade containing oil cells, a ground tissue of loosely arranged cells in which also oil cells are scattered, a regular row of spongy mesophyll below the abaxial epidermis and the vasculature of the leaf.

DISCUSSION

The undifferentiated panel of lamina in *Polyalthia* is a plate of meristematic cells, more or less isodiametric in shape, in which no regular alignment of cells could be determined as in *Liriodendron* (Pray, 1955 *a*), where the meristematic cells of the lamina are narrow, somewhat elongated at right angles to the midrib. The plane of cell division in the ground tissue follows no regular pattern in *Polyalthia* as contrasted with the predominant plane of cell division which is periclinal with respect to the margin in *Liriodendron*. In *Hosta* (Pray, 1955 *c*) the procambium-producing layer is a plate-meristem consisting of more or less isodiametric cells. The plane of division in these cells is also persistently anticlinal with respect to leaf surface and random with respect to each other.

At the earliest stage in ontogeny, the procambial cells of the secondary vein in *Polyalthia* are generally multiseriate and the differentiation occurs progressively. The initially biseriate strand of procambium mother cells, which is of occasional occurrence, soon becomes multiseriate primarily due to divisions in the procambial cells themselves. In *Liriodendron* (Pray, 1955 *a*) also, the secondary vein at inception is multiseriate having been differentiated from a group of adjacently placed cells of the ground tissue and the differentiation proceeds progressively. In *Hosta* (Pray, 1955 *c*) the median strand is the first to appear, the other primary strands being initiated successively, the direction of differentiation being from margin to centre of the blade. The development of these strands proceeds from base to the apex.

In *Polyalthia* the tertiaries originate as uni- or biseriate strips of procambial cells that differentiate simultaneously in a majority of instances.

The differentiation proceeds from the ground tissue which consists of isodiametric meristematic cells. In a few instances a progressive ontogeny was also seen. Under such conditions the differentiation of the procambium proceeded from one secondary vein to another. In *Liriodendron* (Pray, 1955 *a*) it is reported that the intertertiaries originate as delicate strands and consist of uni- or biseriate strips of procambial cells which differentiate simultaneously across the panel. Further, prior to the initiation of all secondaries, the tertiary vein joining the secondaries along the margin begins to differentiate. In *Hosta* (Pray, 1955 *c*), the commissural vein that extends in between the median strands differentiate simultaneously. The cells are elongated at right angles to the primary veins and the procambial cells differentiate simultaneously across the panel as multiseriate structures. The intercostal panel that gives rise to the tertiaries in *Polyalthia* consists of isodiametric cells as in *Liriodendron*. In *Quiina* (Foster, 1952), however, the determination of the procambium from the ground tissue is so early that it becomes fairly easy to identify the uni- or biseriate strips of interveinal parenchyma. In other words, the intercostal meristem in *Quiina* loses its capacity early to produce more procambium unlike in *Polyalthia* and *Liriodendron*. In *Polyalthia*, the tertiary vein grows in width due to the division of the procambial cells or due to the differentiation of procambium from adjacently placed cells of the ground tissue. In *Quiina*, however, the condition under which the teritiary vein differentiates is different. The early demarcation of procambium from the ground tissue with the enclosed uni- or biseriate interveinal parenchyma reveals that the latter tissue is incapable of differentiating into procambium any further. Or, in other words, the determination of the procambial precursors of the tertiary vein in *Quiina* is early and the development is rapid and continuous, whereas in *Polyalthia* the demarcation of the corresponding procambium encloses larger areas of ground tissue in which further differentiation of the quarternary and other veinlets proceeds. Thus, the interveinal ground tissue in *Polyalthia* is capable of differentiating into procambium to a relatively late stage simulating the condition present in *Liriodendron* (Pray, 1955 *a*). *Quiina* (Foster, 1952) and *Hosta* (Pray, 1955 *c*) present certain developmental features common to each other. The area of ground tissue enclosed by two adjacent primaries, from which the procambium of the commissural veinlet is formed, consists of a homogeneous plate of narrow cells which are elongated at right angles to the adjacent primary veins in *Hosta* and this feature simulates to that obtaining in *Quiina*.

In *Polyalthia* and *Liriodendron*, cellular shape in the plate of ground tissue in between the two secondaries is more or less isodiametric and no remarkable change in the shape of cells is noticed during the formation of the

intersecondaries or intertertiaries, whereas in *Hosta*, the initially isodiametric cells become narrow and elongated at right angles to the adjacent primaries when the commissural strands become definable, and revert to the isodiametric shape eventually.

Because of the capacity of the ground tissue to form increasing quantum of procambium till a late stage, the delimitation of the ultimate areoles could not be established with certainty in *Polyalthia*. As Pray (1955 *a*) reports for *Liriodendron*, there is every possibility of an areole being further subdivided by newer procambial connections arising from the ground tissue.

The procambium of the quarternary and minor veins, except the vein ending, develops simultaneously in *Polyalthia* as in *Liriodendron*. In *Hosta*, however, the later-formed strands and veinlets differentiate progressively. The simple, unbranched vein-ending in *Polyalthia* develops progressively like the branched vein-ending in *Liriodendron*. The endings contain xylem in *Polyalthia* and in *Liriodendron*. In *Hosta* (Pray, 1955 *b*) the endings usually contain phloem and in one case it has be shown that the phloem extends beyond the xylem. In *Quiina*, Foster (19) would not arrive at any definite conclusion as to whether phloem element was present in the vein-endings or not.

The differentiation of phloem in *Polyalthia* is continuous and acropetal; xylem also differentiates progressively and continuously. However, instances are not rare where discontinuous nature of differentiation of the xylem is noticed to occur. Similar pattern of xylem development is reported in *Liriodendron*, *Quiina* and *Hosta*. Mention about the discrete strands of protoxylem is made by Pray (1954) in *Nicotiana glauca*, *Ligustrum* sp., *Aucuba japonica* and *Eucalyptus polyanthecus*.

SUMMARY

The venation system of the leaf in *Polyalthia* is pinnate. The procambial precursors of the vein in the leaves originate in the elongated cells of the middle layer, which in turn owes its origin to the adaxial hypodermal layer of cells during the marginal growth of the leaf. Secondary vein development proceeds from the midrib to the margin of the leaf and from base to the apex. The plate-meristem is composed of isodiametric cells at the time of formation of secondary veins. At inception, the secondary vein procambium is multiseriate generally. The development of the tertiary vein procambium is mostly simultaneous and sometimes progressive and differentiates as uni- or biseriate strips. The quarternary vein and minor vein procambium differentiates as mostly uniseriate strips simultaneously. The vein endings, which are simple

and unbranched contain only xylary cells, and develop progressively. The interveinal parenchyma possesses the capacity to produce additional procambial strands for a considerable period in ontogeny. Each areole contains one or two vein-endings, which end in the neighbourhood of the oil cells.

Acknowledgement

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Explanation of Text-Figures

Figs. 1–4. Fig. 1. Transection of embryonic lamina showing the grouped arrangement of the procambial cells. ABXL SIDE—Abaxial side; ADXL SIDE—Adaxial side; O.C.-Differentiating oil cell. Fig. 2. Paradermal section of embryonic lamina showing the progressive differentiation of the secondary vein procambium. Fig. 3. Paradermal section of a lamina showing the simultaneous nature of tertiary vein procambium differentiation. Also a progressive type of differentiation can be noticed here and there. The protoxylem elements have differentiated in the secondary vein procambium. S-Secondary vein procambium. Fig. 4. Paradermal section of a lamina at the time of formation of a vein-ending. This areole contains four differentiating oil cells. All figures, × 375.

Explanation of Plate

Plate VI

Fig. 5. Paradermal section of an embryonic lamina prior to the differentiation of the secondary vein procambium. Note the isodiametric nature of the cells of the plate meristem, × 520.

Fig. 6. Progressive type of differentiation of the tertiary vein procambium. While a biseriate strip of cells has elongated from one secondary vein, a few isodiametric cells at the

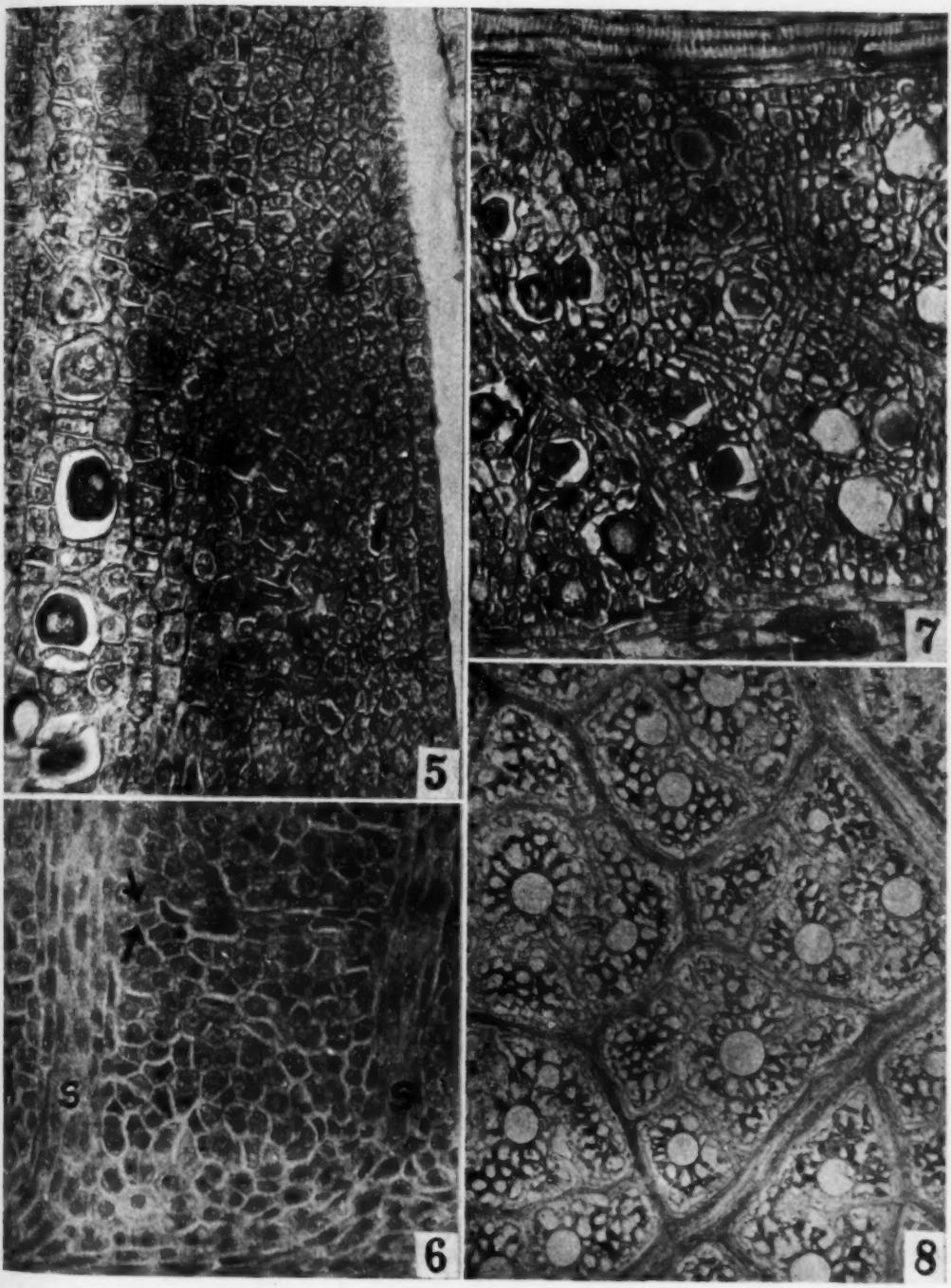
other half (indicated by arrows) break the continuity. These cells may elongate later to establish the connection, × 600.

S.S.—The two adjacent secondary vein procambia which deviate from the procambial midrib seen at the basal portion.

FIG. 7. Paradermal section of the lamina at the time when the quarternary and minor veinlets are formed. The lamina is traversed in a complicated fashion by the procambium of quarternary and minor vein categories. By now the primary xylem is seen to have well developed in the secondary veins, × 440.

S—secondary vein.

FIG. 8. Paradermal section of a mature lamina showing the ultimate areoles and the distribution of the oil cells, × 380.



FIGS. 5–8

AGE DETERMINATION OF THE FISH *THERAPON JARBUA* DAY

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Received July 19, 1960

(Communicated by Dr. R. Subrahmanyan, F.A.SC.)

1. Introduction

The validity of the application of the study of scales and the markings thereon in age determination of temperate fishes like the Gadidæ, the Cod (*Gadus callarias* L.), the mackerel, the pilchard and the Californian sand-dab has been shown by Thompson (1904), Alf Dannevig (1925, 1930), Blackburn (1950) and Arora (1951) respectively. The above authors have established that the number of ' winterchecks ' (rings), which are annual, clearly depicts the age of the fish. But, Frost (1945), working on eels (*Anguilla anguilla*), held that the scale could not be easily interpreted in terms of age as there was the possibility of the failure of the scales in recording the annuli.

The above standards or criteria for measuring age were applied to the Malabar sole by Seshappa and Bhimachar (1951, 1954), who stated that the rings noticed were not quite annual but coincided with the monsoon and, therefore, varied each year. These rings which they call ' monsoonic rings ' are, however, of use in the computation of age, $\pm$ an error of one month in each year. Sundara Raj (1951), who found only incomplete or false rings, emphasised the value of the transverse radii and the length of the scale for computation of age. Thus, a few who applied the annual rings as scale formulæ in age determination of Indian fishes found the method unreliable. It was, therefore, considered worthwhile to assess the age of a fish correctly to months by a suitable method.

2. Material and Methods

Several specimens of *Therapon jarbua* were reared in the laboratory from their early postnatal stage. This fish occurs in brackish and marine waters and attains a maximum length of 25 cm. in Madras. It breeds during the months of November and December. The changes undergone by the fish in the laboratory and in the field were studied side by side during every month for two years (Rajagopalan, 1960). It is important to note that not all the

scales from different parts of the body of the fish are of the same measurement and have the same number of circuli. Hence the scales from the pectoral region above the lateral line alone were chosen for the present study.

3. AGE ASSESSMENT

(*a*) *Scales.*—It is established that *Therapon jarbua* attains an average length of 11·0 cm. with a scale 1·00 mm. long and with 122 circuli during a period of twelve months both in the field and in the laboratory (Rajagopalan, 1960). It was also found that the length of the scale can be related to the number of circuli by the formula $Y = 93{\cdot}7142 - 159{\cdot}84\ (X - 0{\cdot}9171)$ where X is the length of scale as measured vertically from the base line of the spines to the dorsal fringe of the scale, and Y is the number of circuli. The data collected from 50 scales taken from the fishes reared in the laboratory and about 3,000 scales from the fishes netted in the field show that the occurrence of rings is not strictly annual, as the scales of fishes 13·2 cm. long show 2 rings though the fish are actually only 19 months old as seen from specimens reared in the laboratory (Pl. VII, Figs. 2 and 3). The value of recording the actual age of fish by rearing them and obtaining an age equivalent to be used along with the formula given above will be apparent. Whatever discrepancies there may be in rearing fish in small volumes of water in the laboratory as compared with the growth in the natural habitat, it must be admitted that the possession of actual age and growth data under artificial conditions at least for one set of individuals of a species will render methods of age computation from the studies of scales and length frequencies more reliable for the particular species.

(*b*) *Length-frequency studies.*—The usual method of calculating age from length-frequency studies serves as a check on the computation of age and growth from scale measurements, *i.e.*, scale length and number of circuli. The length-frequency distribution of *Therapon jarbua* shows the first two age groups; the mode of group I falling at 10·5 cm. and of group II at 16·0 cm. From the length-frequency histograms it is possible to conclude that growth was uniform during the period of 12 months except for a slack period in the summer months, *i.e.*, March, April and May (Rajagopalan, 1960).

(*c*) *Otoliths and opercular bones.*—Both in the otoliths and the opercular the occurrence of two zones (one opaque alternating with one transparent) or of one calcified ring has been noted as the annual mark (Pl. VII, Figs. 1, 4 and 5). It was observed that a fish 11·1 cm. long with an otolith 4·0 mm. long has two complete zones which mark the first year and another fish 15·6 cm. long with 6·1 mm. long otolith showed four zones indicating the age as two

years (Pl. VII, Fig. 7). Similar transparent and opaque zones as well as the calcified rings are found in the opercular also (Pl. VII, Figs. 6 and 8). These correspond with the length of fish. The evidence of age from the otoliths and opercular is likely to be reliable since the one gathered from the samples collected in the sea agrees with that obtained from fish bred in the laboratory of known age. However, it must be stated that the otoliths and opercular are not so easily removed and that the zones and calcified rings can indicate only 12-month periods and not shorter intervals of time.

4. Conclusion

From the foregoing account, it will be clear that the age of *Therapon jarbua* can be computed correctly to the year and even to the month by counting the circuli in the pectoral scales. It was evident from the measurements of scales that 122 circuli are formed in the first year and 51 in the second year with the scale lengths of 1·05 mm. and 1·61 mm. respectively. But these data are applicable only to the fish studied, *i.e.*, *Therapon jarbua*.

5. Acknowledgments

The author's thanks are due to Dr. C. P. Gnanamuthu for suggesting the investigation and help in preparing this paper, and to Dr. R. Subrahmanyan for his useful suggestions, and to the Syndicate of the University of Madras for the award of a studentship during the tenure of which the present study was undertaken.

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EXPLANATION OF PLATE VII

FIG. 1. Showing otolith (A) with one opaque and one transparent zone. Length of fish 11·1 cm. OP., Opaque zone. TP., Transparent zone.

FIG. 2. Showing an older scale with two rings. C., Circuli. T.R., Transverse radii. I.R., First ring. II.R., Second ring.

FIG. 3. Showing a scale with one ring. R., Ring.

FIGS. 4 and 5. Showing two otoliths under low power.

FIG. 6. Showing opercular bone (1) with two opaque and two transparent zones. Length of fish 15·6 cm. OP., Opaque zone. TP., Transparent zone.

FIG. 7. Showing otolith (B) with two opaque and two transparent zones. Length of fish 15·6 cm. N., Nucleus. OP., Opaque zone. TP., Transparent zone.

FIG. 8. Showing opercular bone (2) with one opaque and one transparent zone. Length of fish 11·1 cm. OP., Opaque zone. TP., Transparent zone.

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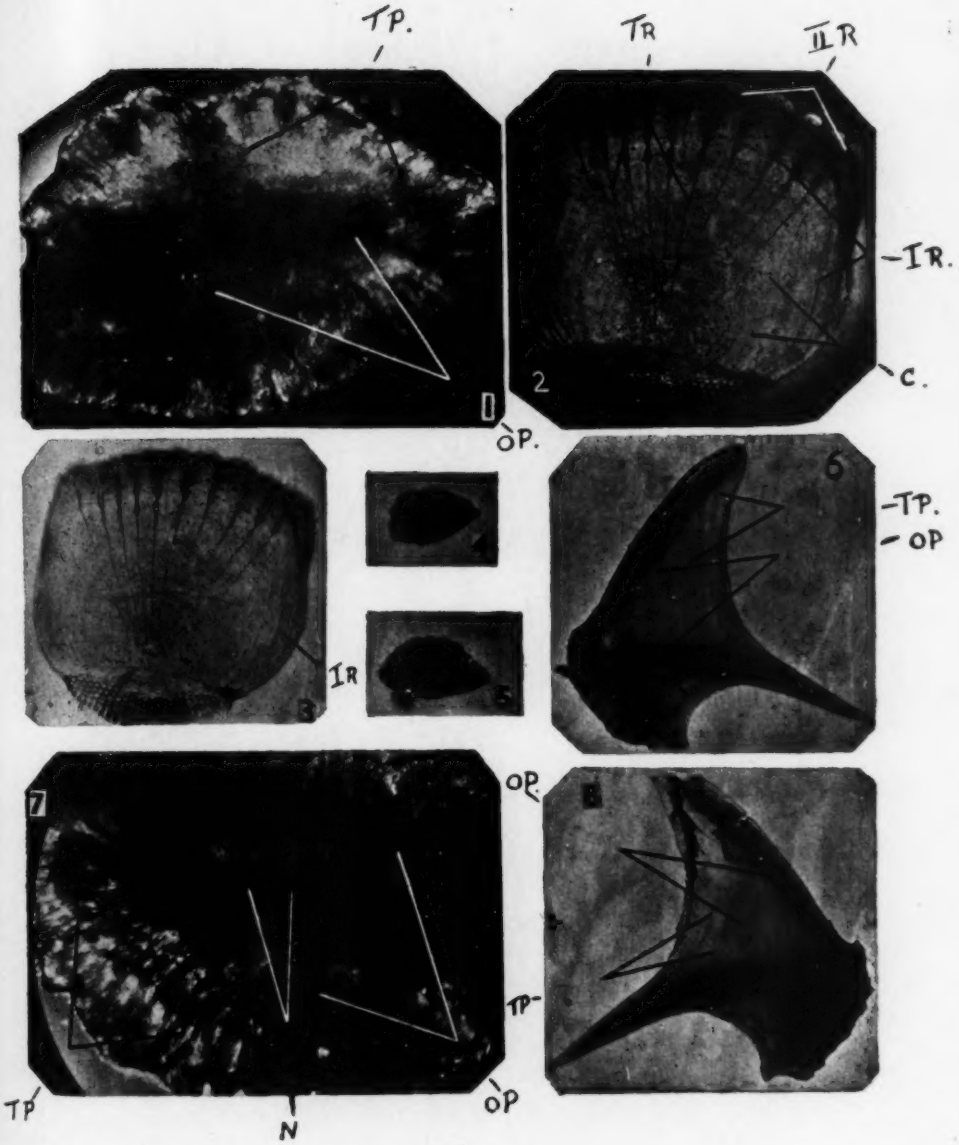

FIGS. 1–8

NOTE

In the paper "Studies in Cellular Slime Moulds from Indian Soils. I. On the Occurrence of *Dictyostelium mucoroides* Bref. and *Polysphondylium violaceum* Bref." by J. N. Rai and J. P. Tewari published in Vol. LIII, No. 1, January 1961, on page 8, the following reference may kindly be added:—

Agnihothrudu, V. .. "Occurrence of Dictyosteliaceæ in the rhizosphere of plants in Southern India," *Experientia*, 1956, **12**, 149.

HIMALAYAN OROGENY AND SEDIMENTARY CYCLES*

By J. Swami Nath

(Geological Survey of India)

Abstract

In the outer Himalaya, during the Cenozoic Era, the quiescent phases, between the orogenic impulses, are marked by three successive periods of sedimentation. The principal sedimentary facies are: (1) 'Black shale facies' (Subathu) of the Eocene period followed by (2) 'flysch facies' (Lower Murree-Dagshai) during the lower part of Lower Miocene Epoch, and finally replaced by (3) 'Molasse facies' (Siwaliks) during the Middle Miocene to Pliocene. This succession of facies points to a natural consanguineous association of a group of sediments and such sedimentary cycles have been observed in geosynclinal areas in other parts of the world.

The disposition of the Tertiary basins of sedimentation is between the craton (Peninsular mass) to the south and rising mountains in the Ortho-geosynclinal belt (Extra-Peninsula) to the north, the latter being the source of sediments. The sediments thicken towards the Himalayas and become thin towards the craton. Thus, the flysch and molasse filled geosyncline along the outer Himalaya corresponds to an 'exogeosyncline' (Kay, 1951).

Introduction

The Cenozoic Era, in the Extra Peninsula, witnessed the great edifice of the Himalayas being built up by stupendous earth movements punctuated by periods of quiescence. The passive phases, between the orogenic impulses, are marked by sedimentation controlled by varying degrees of tectonism that determined the *kinds* of sedimentary products. The object of this paper is broadly to classify and describe the principal Tertiary sedimentary facies, in the basins of deposition in the outer Himalaya (towards the Peninsular side of the Extra Peninsula, excluding Sind and Assam regions) and to draw attention to the manner in which such facies commonly follow one another.

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* Paper presented to the Symposium on Tectonics, December 1959.
With kind permission of the Director, Geological Survey of India.

In this study some conjectures, on the domains of sedimentation represented by the principal facies, are inevitable; but relevant data from the sedimentary records are presented here, from the Eocene to L. Pleistocene, and an attempt is made to classify these domains. These generalizations and interpretations would, of course, need confirmation by further detailed studies of different areas.

Krishnan (1956; p. 74) stated that the Tertiaries of the Himalayas could be divided into deposits of three or four successive periods of sedimentation, each commencing with, and culminating in, a mountain building movement. The four orogenic periods are: Upper Cretaceous, Upper Eocene, Lower to Middle Miocene and Late Pliocene to Lower Pleistocene and the corresponding sedimentary formations being the Ranikot-Laki-Kirthar-Subathu, the Murree-Dagshai-Kasauli and the Siwaliks (*see* Map).

EOCENE

The Eocene is represented by a shallow marine facies on the southern side of the Main Himalayan Range from the Salt Range in the west to as far as east of Naini Tal (Krishnan, 1956; p. 75).

A brief summary is given of the Eocene Sections, in different parts of the outer Himalaya, in so far as is pertinent to this study.

Salt Range.—The Ranikot series of Lower Eocene age comprise sandstones and carbonaceous and gypseous shales, with subordinate and nodular limestones. The Patala Shales of Upper Ranikot beds are grey shales often carbonaceous and are reported to be alum-bearing due to the action of sulphuric acid derived from decomposing pyrite in the shales (Krishnan, 1956; p. 470). The Laki Series overlying the Ranikot is mainly a calcareous formation.

Pir Panjal.—Ranikot is represented by cherty, flaggy limestones; alternating thin-bedded, slaty and massive grey splintery limestone with interbedded phyllitic slates. The Laki Series—"Chharat Series"—consists of carbonaceous pyritous shales, dense jasper-like quartzite (metasomatically replacing bituminous limestone); followed upwards by grey calcareous shales with lenticular, semi-nodular and highly bituminous black limestone (Wadia, 1928; pp. 258–59). The Laki limestones are highly bituminous with a sooty black colour and give out a fetid odour when struck.

In the Eocene section of Khandar olive-green shales with lenticular coal seams, marly shales, pyritous and carbonaceous shales with iron stone

have been recorded (Wadia, 1928; p. 262). Similar grey and green pyritous and carbonaceous shales with nummulitic limestones are seen near Riasi (Jammu District) and these are considered to be homotaxial with the Subathu beds of Simla Hills.

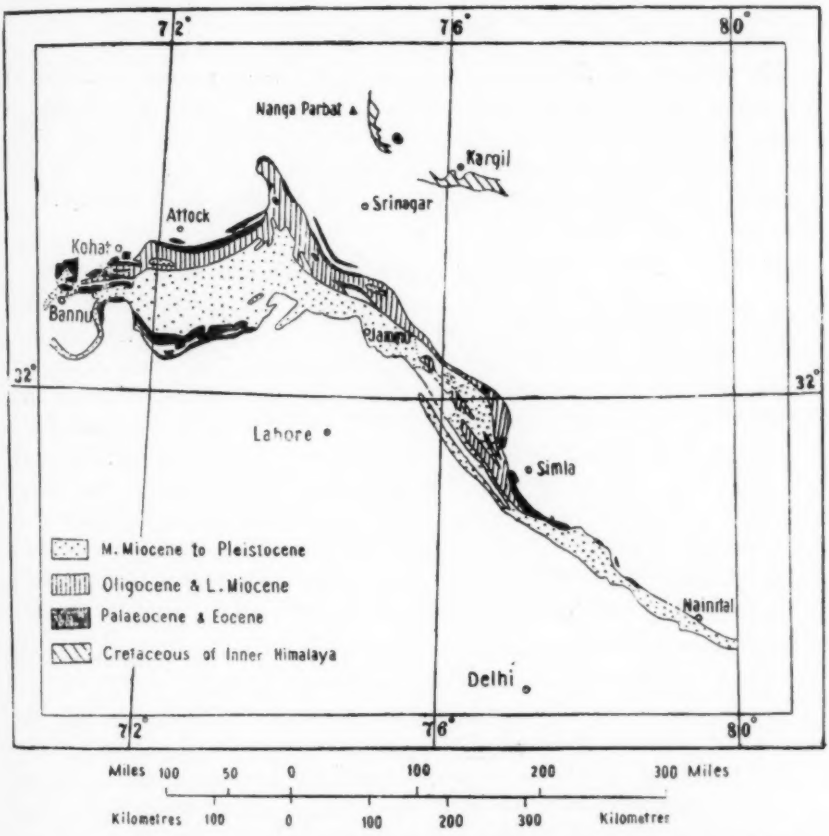

Fig. 1. Geological Sketch Map Showing the Tertiary Formations of the Outer Himalaya.

Bilaspur-Sundernagar Area (Simla Hills).—V. H. Boileau and the writer observed in the Bilaspur–Sundernagar area, north of Simla, marine Eocene beds (Subathu) comprising dense lenses of limestone and maris with black shales. These shales are pyritic and polybituminous and are associated with thin beds of black quartzite followed upwards by lenticular thinly bedded limestones containing a few nummulites.

Subathu Area (*Simla Hills*).—The Subathu of this type area was described by H. B. Meddlicott (1861; p. 11). The beds are calcargillites, with subdued colours and fine textures and weather as splinters. Thin beds of pure hard limestones are also present.

The belt of Eocene rocks continues south-eastwards into Garhwal along the foot-hill zone of the Himalayas.

Environment of Deposition of Eocene Beds.—The total thickness of the Eocene sections observed account for no more than 2,000 ft. (maximum) and are complete in most parts of the Sub-Himalayan belt. The occurrence of carbonaceous and pyritous shales in the stratigraphic record of the Eocene is striking and is of significance in attempting a sedimentary and tectonic analyses.

Krishnan (1956; p. 462) mentioned that the end of the Cretaceous period was marked by widespread regression in the Extra-Peninsula due to the late Cretaceous orogeny, that initiated the important physiographic changes which became accentuated in the Cenozonic Era. This regression of the strand line in early Eocene may have left behind relict shallow seas or silled or barred basins in which free access to open ocean became restricted. The Eocene beds appear to have been laid down in such basins. In such an environment, various degrees of stagnation of bottom waters may ensue depending upon the extent to which circulation of the waters was impeded. Under humid climate, bituminous and pyritous shales with dense dark limestones (not very thick) are known to accumulate giving rise to 'Black Shale Facies' (Pettijohn, 1956; p. 622; Krumbein and Sloss, 1956; p. 182).

The occurrence of gypseous shales in some sections appear, on the other hand, to indicate restricted circulation in the basin and rapid evaporation under arid climates. Pettijohn (1956; p. 485) pointed out that the oxidation of pyrite in the black shales may give rise to acid sulphate waters that react with limestones in the sequence giving rise to gypsum, although most gypsum deposits may not be of this origin. The gypsum occurrences in the Lower Ranikot of the Salt Range may be due to the action of sulphate waters on limestones (p. 3). In the Paradox Formation (Pennsylvanian) of Eastern Utah black shales are associated with evaporites. In this connection Krumbein and Sloss (1956; p. 182) point out "Recurrent freshening of waters may occur, depending upon the magnitude of the barrier and the depth of the restricted sea. As a result, euxinic associations may occur interbedded with normal marine deposits. Under some conditions black shales may be associated with evaporites....." Discussing the environment of deposition of the Lower Chharat Series in Kala Chitta,

Pascoe (1912; pp. 344–45) stated that he believed that this series was, in all probability, deposited in land-locked lagoons of salt-water sufficiently concentrated to cause deposition of gypsum and the Upper Chharat Epoch represented a return of open-sea conditions. In the Permian basin of mid-continent region (U.S.A.) the transition from euxinic sediments to those of desiccation is not extremely sharp (Roth, 1942; p. 1666).

Whether the occurrence of gypseous beds in the Eocene succession is to be ascribed to fluctuations of restricted and open-sea conditions during the period or to action of sulphate waters by the decomposition of pyritous shales in the sequence; one point appears obvious that pyritous and bituminous black or grey shales are, in all probability, indicative of euxenic sediments. The Eocene sediments, therefore, accumulated under an environment of low oxidation-reduction potential giving rise to "Black Shale Facies".

Oligocene—Lower Miocene

The second mountain building paroxysm during the end of the Eocene period had the effect of driving out the sea from most of the Himalayan area except along the outer Himalaya (Krishnan, 1956; p. 484). In this basin, from Potwar in the west to Garhwal in the east, the Murree-Dagshai-Kasauli formations were laid down.

Potwar Area.—The Lower Murrees are purple and dark green, fine-grained sandstones that alternate with dark, red and purple clays and shales. Pseudo-conglomerates are a common occurrence but true conglomerates are rare. The basal beds contain derived nummulites (Cotter, 1930; p. 107).

North-West Punjab.—The Murrees include hard sandstones of pale grey or purplish colour crowded with obscure plant impressions resembling fucoids associated with annelidian markings (Wynne, 1877; p. 118).

Kashmir-Jammu.—In Poonch State (Wadia, 1928; p. 270) the Lower Murrees are represented by hard fine-grained, non-micaceous, ferruginous, deep red, purple or grey slab-like sandstones; pseudo-conglomerates, red and purple splintery shales and some green phosphatic shale with thin argillaceous limestone partings. This sequence is followed conformably by red purple, grey and buff shales with coarse micaceous grey sandstones.

In the Fatehpur Section (Wadia, 1928; p. 265) the purple sandstone and shale sequence contains black thin-bedded foraminiferal limestone. The conditions of sedimentation in this area point to a sequence of rapidly varying conditions due to a temporary inroad of a shallow sea (Wadia, 1928; p. 266).

The Murree belt of Poonch extends past Murree hills along the foot of the Margala and Kala Chitta Hills, beyond Indus, to as far as Kohat.

The Murrees are as usual purple-coloured with an endless alteration of red and purple clays with purple and grey thick or thin sandstones. Pinfold (1918–19; p. 152) also refers to purple sandstones and shales in the Murrees.

In the Soan Syncline the Lower Murrees are hard, fine-grained, non-micaceous purple and grey schists with deep red and purple splintery and "semi-concentric shales" and pseudo-conglomerates. The Upper Murrees are coarse, soft, "Siwalik-looking" sandstones interbedded with purple, splintery and concretionary shales of typical Murree Facies (Wadia, 1928; p. 338).

Bilaspur-Sundernagar Area.—The Lower Murree Facies is represented by the Dagshai and the Upper Murree by the Kasauli. There are several bands of green sandstones separated by maroon shales which passes upwards into a zone of maroon shales with thin sandstones. The sandstones are flaggy in places. At the top there are several micaceous sandstones with maroon shales or shaly marls in sandstone bands. Boileau, Kohli and the writer (1953) have referred to the Dagshai as "Crimson Flysch".

Simla Area.—At Dagshai (the type area) the shales are deep red in colour and the sandstones dark purple. Meddlicott (1861; p. 12) refers to these as the "Red rocks". The Dagshai are followed by the Kasauli beds in which the arenaceous component increases to almost total exclusion of any other.

Garhwal Area.—Rocks similar in lithology to the Dagshai of the Simla area are known to occur in Garhwal also (Middlemiss, 1887).

ENVIRONMENT OF DEPOSITION OF MURREE–DAGSHAI–KASAULI SEDIMENTS

The lower Murree and Dagshai sediments are thought to be brackish-water while the Upper Murree and Kasauli of freshwater origin (Krishnan, 1956; p. 487). Pascoe (1912; p. 349) considered the Murree sedimentation to form an intermediate stage from marine Nummulites to fluviatile Siwaliks, and the Lower Murree sediments to have been laid down in lagoons or lakes. Meddlicott (1861; p. 12) stated: "The series seem to represent one uninterrupted sequence of formation, the deposits of tranquil and deeper waters being transitionally succeeded by accumulations of sand, in the uppermost of which we find unmistakable evidence of the immediate proximity of land".

The author, with his senior colleague Boileau, has carried out a rapid reconnaissance of the Dagshai rocks in Bilaspur-Sundernagar area and designated these beds as 'Crimson Flysch' (V. H. Boileau, Kohli and Swami Nath, 1953). The observations of some of the previous workers are also cited here to support the idea that these sediments have the characters of 'flysch' as defined in the Alpine and other regions of the world during an early period of mountain building. The observed characters in the Murree-Dagshai sequence in the outer Himalaya are compared in the following statement with well-established characters of flysch sediments according to well-known authorities.

Descriptions of Lower Murrees/Dagshai	Other Authorities of Flysch
1. The occurrences of fucoids (Wynne, 1877; p. 118).	1. (*a*) Hierogyphs or fucoids are reported in some flysch (Sujkowski, 1957; p. 545). (*b*) ".... rich in organic and inorganic sole markings (=hieroglyphs)" (Dzulynski *et al.*, 1959; p. 1089).
2. Absence of carbonate rocks. Concentration of the calcareous matter in solution at times reached the stage of precipitating beds of impure limestone (Wadia, 1949; p. 433). In the Fatehpur Section, limestones are present which are only local.	2. "Beds of calcareous pelagic marl or, less commonly, limestone are also known; they are also limited to some sub-zone but where present are persistent. Such beds do not obliterate the flysch character" (Sujkowski, 1957; p. 547).
3. (*a*) Pseudo-conglomerates are common (Cotter, 1930; p. 107) and true conglomerates rare (Anderson, 1927; p. 681). (*b*) "The deposit (Pseudo-conglomerate) is most commonly composed of a sandy matrix containing lenses of siltstone and full of a variety of small, pebble-like inclusions of slitstones and less often sand-	3. (*a*) Pellets of shale or galets of half indurated shale are known and in place assume the appearance of a conglomerate (Sujkowski, 1957; p. 544). (*b*) The heavier more massive beds may enclose randomly orientated fragments of shale or slate presumably derived from the associated slates (Pettijohn, 1956; p. 302).

Descriptions of Lower Murrees/Dagshai	Other Authorities of Flysch
stones, of the same type of as those forming the system itself and with little doubt derived from it" (Anderson, 1927; p. 680).	
(*c*) "This strange type of deposit (Psuedo-conglomerates) presents numerous interesting problems deserving special investigation and discussion. The writer believes that it represents frequently recurring times and places in which beds in the system were subjected to fairly prolonged exposure, to surface concentration of cementing agencies, and to drying and cracking with the resultant reworking, transportation and deposition by wind and running water" (Anderson, 1927; p. 281).	(*c*) "The sandstones are micro-breccias or grits containing numerous shale fragments, and are not the products of normal bottom currents. They appear to record infrequent, somewhat catastrophic, incursions of slump-generated turbidity under flows. Such flows transfer sediments once deposited in comparatively shallow water to a deep still-water environment" (Pettijohn, 1956; p. 615).
4. "Although the finer phases and occasional lenses approach true clay, most of the deposits differ from clay in characteristically, containing minute gritty grains..... It differs from the shale in having a massive character which is wholly predominant over the occasional lamination" (Anderson, 1927; p. 678).	4. The texture of these sediments in all essential details appear to resemble graywackes (Kuenen and Migliorini, 1950). Most beds (graywackes) lack any internal stratification and are commonly massive (Pettijohn, 1936; p. 302).
5. "No fossils are observed in the Dagshai group except fucoid marks and worm tracks, fossils which are of no use for determining either the age of the deposits or its mode of origin" (Wadia, 1949; p. 260).	5. There are signs of worm activity and burrowing in the mud. Almost no shells are preserved and macrofossils rare (Sujkowski, 1957; p. 546).
Occurrences of annelidian markings are known (Wynne, 1877; p. 118).	

Descriptions of Lower Murrees/Dagshai	Other Authorities of Flysch
6. The red colour of the rocks points to heavy oxidation and rather dry conditions in the areas from which the sediments were derived (Krishnan, 1956; p. 488).	6. "Some Flysch Series exhibit evidence of oxidising conditions, though such conditions do not seem to have been typical of flysch sedimentation. Some parts of the thick flysch series were deposited in the presence of free oxygen···". The Lower Cretaceous Flysch in the Carpathian may be mentioned (Sujkowski, 1957; p. 549).
7. "A strong purple colour pervades the whole lower portion of this group, which shows an endless alternation of red and purple clays with purple and greyer thick or thin sandstones and concretionary earthy or slightly calcareous bands" (Wynne, 1877; p. 118). "···· predominantly silty stage, at least some hundreds of feet thick, composed of grey, reddish and purplish siltstone interbedded with grey and greenish-grey sandstone (Anderson, 1927; p. 683).	7. "The bedding is well marked, uniform, and rhythmic. The principal material is shale or silty shale regularly interbedded with beds of graywackes. The strata are characteristically described as rhythmites" (Pettijohn, 1956; p. 615).
8. "The series seems to represent one uninterrupted sequence of formation, the deposits of tranquil and deeper waters being transitionally succeeded by accumulations of sand" (Meddlicot, 1861; p. 12).	8. "The shales apparently accumulated relatively slowly; their accumulation being periodically interrupted by the instantaneous deposition of sandy beds" by turbidity underflows (Pettijohn, 1956; p. 615).

Though the Murrees and Dagshais have not been described as flysch by previous workers, it is obvious that there are striking similarities between them and the features now accepted as characteristic of flysch elsewhere. It is only during the last decade or so that flysch sedimentation has been carefully analysed by leading sedimentologists and their characters, environment and conditions of formation properly understood. (Kuenen and Migliorini, 1950; Kuenen and Carozzi, 1953; Pettijohn, 1956; p. 615; Sujkowski, 1957, pp. 543–53, etc.; Dzulgynski *et al.*, 1959).

If the facies is one of flysch it follows that the lower Murree and Dagshai are marine sediments laid down in a geosyncline in an earlier stage of mountain building. The thickness of these rocks is difficult to determine, due to their having been involved in folding and thrusting in subsequent movements. The total thickness of Murree-Dagshai and Kasauli is estimated between 5,000–8,000 ft. in N.-W. Punjab (Wynne, 1877; p. 118), about 6,000 ft. in Poonch State (Wadia, 1928; p. 270) and about 3,000 ft. in Simla Hills. In the Bilaspur area, the Dagshais are involved in tight folding in the para-autochthonous belt and it is not possible to determine its true thickness. Nevertheless, it is well over 3,000 ft. These thicknesses are compatible with geosynclinal sediments.

During the Upper Murree and Kasauli times the argillaceous sequence of Lower Murree and Dagshai gave place to an arenaceous sequence, increasing upwards in coarseness. Pinfold (1918–19; p. 153) referred to Upper Murree beds as "Siwalik type" and in the Soan Syncline also Wadia (1928; p. 338) has observed "Siwalik-looking sandstones" in Upper Murrees. Meddlicott (1861; p. 12) referring to the Kasaulis has remarked on the arenaceous element increasing to the almost total exclusion of any other. It is obvious, therefore, that during the upper part of Lower Miocene epoch the flysch facies gave place to the molasse facies or to a transition between the two.

MIDDLE MIOCENE TO LOWER PLEISTOCENE

The third episode of mountain building activity occurred during the Middle Miocene and there was the final retreat of the sea from the whole of the outer Himalaya and paralic sedimentation dominated the scene. It was stated earlier that in the Upper Murree times the transition from flysch had already set in and towards Middle Miocene the change appears to have been complete. In the fore-deep formed south of the rising mountains the Siwalik sediments were laid down, characterised by intense terrigenous alluviation, the sediments being derived from the rising mountains to the north, brought down by numerous rivers.

The Siwalik system comprises sandstones, grits, pseudo-conglomerates, conglomerates, clays and silts. The sandstones are current-bedded and show lateral variations.

The Siwalik system and other systems homotaxial with it have received considerable attention mainly due to the rich harvest of mammalian fossils gathered from them and have been described in great detail in many sections along the outer Himalaya (Wadia, 1949, pp. 266–70; Krishnan, 1956, pp. 504–07). In the Bhakra Reservoir area, the Lower Siwaliks are thick

sandstones with beds of pseudo-conglomerates, with subordinate red clays and marls followed conformably upwards by the Middle Siwaliks (Nagris) with thin sandstones, red clays and marls. They are conformably overlain by a dominant "sand rock facies" (Dhok Pathans) with thin grey or red clays and pebble beds while conglomerates appear on top (Tatrot). The lateral variations met with in the Siwaliks are of regional significance; hence a type of section is difficult to define. However, the gross sedimentary characteristics in the Siwaliks are more or less uniform throughout the basin of deposition—the lower part being arenaceous and argillaceous, giving place to a dominant arenaceous sequence with pebble beds in the upper part and finally to conglomerates on top. There is, therefore, a general coarsening upwards. The sandstones in the Siwaliks are highly micaceous and appear to be sub-greywackes. The pebbles and boulders, in the Bhakra area, consist of quartzites (pink varieties being derived from the Shali sequence in the allochthonous belt), basic rocks and a few granite pebbles. Middlemiss (1887; p. 112) has already pointed out the source of the materials in the Siwaliks to be the higher Himalayan range.

The freshwater origin of the Siwalik sediments is a recognised fact. The sandstones and clays appear to be immature products of rapid denudation derived from the Himalayas (Middlemiss, 1887; p. 2). Nearly a century ago, Meddlicott (1861; p. 25) had the keen insight to point out the general similarity of the Siwaliks to the Swiss Molasse in texture and composition. There is little doubt that the Siwaliks are paralic sediments and represent a "Molasse Facies" in the Orogenic belt, which has itself been deformed later (Pettijohn, 1956; p. 618).

The thickness of this Molasse in the Sub-Himalayan, range from over 10,000 ft. to about 17,000 ft.

At the end of the Pliocene, the Sub-Himalayan Molasse was folded and thrust towards the Peninsula shallowing the foredeep and shifting it further south. Minor movements, including the thrusting and uplift of the Pir Panjal range, continued during the Pleistocene and recent times. The valley of the Ganges and Brahmaputra are filled with Mio-Pliocene, Pleistocene and Recent sediments (Krishnan, 1953; p. 56).

Analysis of Sedimentary Facies

The 'Black Shale Facies' of the Eocene period, followed by 'flysch facies' in Lower Murree-Dagshai times and finally by the 'Molasse Facies' in the Middle Miocene to Pliocene point to a natural consanguineous association of a group of sediments (Pettijohn, 1956; p. 636). This succession

of facies is representative of one geosynclinal cycle and has been recorded in areas of geosynclinal sedimentation in other parts of the world. However, in some areas, two cycles have been recognised (Pettijohn, 1956; p. 641). If, however, the interpretation, of Lower Murree-Dagshai sequence, as flysch, is proved to be incorrect by later detailed work, it follows that in the Outer Himalaya there is an exception to the normal geosynclinal cycle where flysch is not represented but Molasse follows the 'Black Shale Facies' directly. Evidence in support for or against the interpretation will be a valuable contribution to our understanding of sedimentary facies of our geosynclines.

Prior to the Tertiary diastrophisms, in the Cretaceous period, the Tethys geosyncline formed the eugeosynclinal belt of that period in the Himalayan area and beyond (due to crustal shortening in later orogenies its geographical limits cannot be determined) as indicated by the presence of radiolarian cherts (Jacob, 1954), flysch with exotic blocks (Krishnan, 1953; p. 49), volcanic ejectmenta (Wadia, 1949; p. 197) and ultramafic intrusions during the Late Cretaceous Orogeny. There is no doubt that geanticlines or tectonic ridges raised in this orthogeosynclinal belt were the source areas of sediments during the Cenozoic Era. The disposition of the Tertiary basin of sedimentation is between the craton (Peninsular mass) to the south and rising mountains of the Orthogeosyncline to the north. The Tertiary sediments thicken towards the Himalayas and become thin towards the craton (Anderson, 1927; pp. 683 and 697). The Tertiary Geosyncline corresponds to an 'Exogeosyncline' as defined by Kay (1951; pp. 87–107). During the Lower Murree-Dagshai times this Exogeosyncline received 3,000–4,000 ft. of flysch sediments and during Upper Tertiary times 15,000–18,000 ft. of Molasse detritus. Kay (1951; pp. 17–20) has cited the Upper Ordovician Cincinnatian Series in Eastern America and the succeeding Silurian Molasse and Middle and Upper Devonian Flysch sedimentation in Exogeosynclines. This flysch and molasse-filled geosyncline of the Tertiary, along the outer Himalaya, may be called the 'Tertiary Exogeosyncline'.

The filling and deformation of a geosyncline may be complex and each has its own individual history and comparisons between one geosyncline and another can only be made on broad generalisations. It is significant that in the Extra-Peninsula as in North America (Kay, 1951) or in Eastern Australia (Swami Nath, 1958) with the deformation of Orthogeosynclines, detritus was redeposited in a later order Exogeosyncline, thereby indicating their 'Cannibalistic' nature as aptly expressed by Krynine. The deforma-

tion of Tertiary Exogeosyncline yielded detritus to the Gangetic trough which is now being filled.

Whether from the point of view of a driftist or an accretionist, the tectonics and the attendant geosynclinal cycle in the Outer Himalaya, in the Cenozoic Era, is an exciting subject of geologic study. The manifestations of gigantic earth movements in the Extra-Peninsula appear to signify to the driftists, the collision of the drifting Peninsula with the Asian landmass. On the other hand, to the accretionists, the development of Intracratonic geosynclines or Exogeosynclines in the Tertiary appears to be an effort to knit the Craton (the Peninsula) with earlier Orthogeosynclinal belts (the Extra-Peninsula) during the Quarternary Era.

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STRUCTURE AND TECTONICS OF THE MANGANESE ORE BELT OF MADHYA PRADESH AND ADJOINING PARTS OF BOMBAY*

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Introduction

The manganese ore belt of Madhya Pradesh and adjoining parts of Bombay forms a general ENE trending arcuate belt, 130 miles long and 20 miles wide, extending from Chindwara District in the north-west, through Nagpur and northern Bhandara Districts in the middle to Balaghat District in the

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north–east. It is underlain principally by a succession of intensely deformed and metamorphosed pre-Cambrian sediments included by L. L. Fermor in the Sausar Series. Amphibolites, some para-gneisses, migmatites, orthogneisses, granite plutons, pegmatites and vein quartz, all presumably pre-Cambrian in age have either been mixed up or emplaced later in the Sausar Series. Along the southern margin of the belt hypersthene-bearing charnockitic rocks occur apparently with intrusive relationship to them. The thin and discontinuous Lameta formation of late Cretaceous age, and the succeeding Deccan Trap basalt of late Cretaceous-Eocene age overlie the Sausar Series with profound unconformity, and are the only other important rock units of this area.

The structural trend of these pre-Cambrian rocks conforms to that of the Satpura range in the north, and the detailed mapping of over 2,000 sq. miles in this belt has yielded data on the structural and tectonic history of the Satpura orogeny that deformed the rocks of this area. A synthesis of the geology of various parts of the manganese ore belt indicates that the Satpura orogenic cycle was much more complicated than what has been realized so far. The 'nappe' structure of Deolapar, worked out by W. D. West (1936), has been confirmed and extended into the adjoining Balaghat District, and additional nappes have been recognized and mapped along the northern part of the belt. At least two definite periods of deformation are postulated for the present structural disposition of the rocks. 'Cross-folding' of the earlier folds indicating a late stage deformation has been distinguished in the Sausar Series. The present paper presents briefly the complicated structural and tectonic history that affected this area during the Satpura cycle.

The results presented here are the outcome of three or four seasons fieldwork in the manganese ore belt by the writer and some of his colleagues —S. Narayanaswami, S. C. Chakravarty, K. D. Shukla, M. R. Subramaniam, V. Venkatesh and G. V. Rao under the general guidance of John A. Straczek.

GEOLOGICAL STRUCTURE

General statement.—The rocks of the Sausar Series are intensely folded in isoclinal and recumbent folds along E-W axes which generally plunge eastward or westward at low to moderate angles. The folds are generally overturned northward with their axial planes dipping steeply southward at 60°–80° along the southern part of the belt, and flattening to moderate southward dips of 30°–50° along the central parts where the isoclinal folds are recumbent. In parts of Balaghat District at the north-eastern end of the belt, the recumbent folds are very flat and are overturned to the south

with low northward dips of 10°–30°. Along the northern margin of the map area, the recumbent folds are found to be thrust over older rocks in the form of thrust sheets and nappes. The belt is traversed by some major steeply dipping thrust faults trending parallel to the strike, and by minor transverse faults. The isoclinal folds of the southern belt and the recumbent folds and thrust sheets of the northern belt have an *en echelon* disposition as the folds themselves show successive northward shifts when followed to the east and north-east. A similar reverse pattern of northward shifts is also apparent in Chindwara District towards the west. The structure of the belt is further complicated by the refolding or cross-folding of the earlier fold axes of the isoclinal and recumbent folds and thrust sheets. The axes of these cross-folds plunge at low to moderate angles to the west and south-west. Granite plutons and ortho-gneisses are generally found emplaced along the axes of these late cross-folds.

Folds and Thrust Sheets

The structure of the belt may be described under the following four divisions:

1. Southern belt of overturned, isoclinal folds.
2. Northern belt of recumbent folds and thrust blocks or nappes.
3. Central belt of gneissic formations of the nature of crystalline axis with narrow and linear outcrops of infolded schists.
4. Regions of refolding or cross-folding and associated granite plutons.

(1) *Southern belt of isoclinal folding.*—This belt, characterized by steeply dipping, overturned, isoclinal folds extends along the southern portion of the manganese ore belt from Kelod-Salai-Parseoni in north-western Nagpur District, through Mansar-Goguldoho in northern and north-eastern Nagpur District and Dongari Buzurg-Chikhla-Bhajiadand-Waraseoni region in northern Bhandara and Balaghat Districts to Bharweli-Ukwa region in eastern Balaghat District. The axes of these folds trend WNW–ESE to east-west in Nagpur District, and gradually veer to ENE and NE in Bhandara and Balaghat Districts. They plunge at low angles of 20°–30° eastward, though westerly plunges are also noticeable at intervals due to the cross-folding.

(2) *Northern belt of recumbent folds, thrust blocks and nappes.*—This belt extends from Sapghota–Ambajhiri in north-western Nagpur through Deolapar region (W. D. West, 1936) in northern Nagpur District to the Sonawani and the Dhansua R.F. in northern and north-eastern Balaghat

District. The belt is characterized by at least four thrust blocks or nappes which have not yet been connected together along their strike. These are (1) Sapghota thrust block, (2) Ambajhiri thrust block, (3) Deolapar nappe and (4) Sonawani thrust block. They consist of younger rocks of the Sausars (Chorbaoli to Bichua stages) which have been thrust over the Tirodi biotite-gneiss, and form steep to moderate dipping overturned, isoclinal folds and flat-dipping recumbent folds whose axes are conformable to the regional fold axes. In the Sapghota-Ambajhiri and Deolapar thrusts, the thrust plates reveal steep to moderate southerly dips along their southern margins and low to flat dips along their northern margins. The Sonawani thrust block shows low to moderate dips to the north, but the northern limit of the thrust has not yet been mapped. The folds within the thrust blocks or nappes are generally doubly plunging synclinal structure which are themselves folded, recumbent folds; the succession of rocks in the case of Ambajhiri and Deolapar nappes is reversed, but is normal in the case of Sonawani and adjacent thrust blocks.

3. *Central belt of gneissic formations with narrow infolded schists.*— This belt consisting of extensive stretches of Tirodi biotite-gneiss and characterized by numerous narrow, linear, infolded runs of schists occupies the region between the two structural divisions described above and appears to represent the central crystalline axis of the tectonic framework. An extensive area of this belt is exposed in Balaghat District between the Bawanthari River in the south-west, Tangla and Karwahi RF on the west and Kurai and Sonawani RF in the north and extends through the alluvial plains of Katangi, Waraseoni and Balaghat up to the Dhansua RF and other hill tracks in north-eastern Balaghat District. The individual outcrops are mostly less than 200 ft. in width and some are four to five miles in length, and occur within the biotite gnesis with a general ENE-WSW to NE-SW regional trend. They are considered to be remnants of steep to flat dipping infolded, recumbent, refolded folds, consisting chiefly of Mansar muscovite schist and the associated manganese ore horizon and Sitasongi quartz-muscovite-schist. The Tirodi–Sukli–Garra area is underlain by the largest number of these infolded runs of Mansar schists and manganese ore bodies in an apparently inverted sequence.

There are three other detached areas that form part of this belt: (1) An east-west area in the Warpani R.F. in north-western Nagpur District, (2) An east-west area extending westward from Mangarli to west of Paunia in Northern Nagpur District, and (3) A small area extending westward from Aoleghat in north-eastern Nagpur District. The area to the east of Mangarli is characterized by numerous infolded Mansar schist outcrops.

4. *Regions of Cross-folding and refolding.*—Evidences are found throughout the manganese ore belt for a late stage deformation which has affected the earlier folds to varying degrees. These later folds which may be described as cross-folds are classified into the following groups:

(1) These cross-folds have their axes at about 45° to the axes of earlier folds, and plunge at moderate angles in the opposite direction. They are found in force in the central part of the belt from Ramtek in Nagpur District to Pusada in northern Bhandara and Tirodi area in Balaghat District. The most characteristic one in this region is the Alesur–Susurgeh–Pusada cross-fold which plunges at 30°–50° south-west, whereas the earlier isoclinal folds plunge at 25°–30° east.

(2) Those which are parallel to the earlier ones, but their axes plunge in the opposite direction generally at 20°–30° west or south-west. Examples of this type are found in the Goguldoho–Junewani–Suwardhara–Parseoni region of northern Nagpur District, and along the Chandpur quartzite range in northern Bhandara District.

(3) Those having their axial planes parallel to the main folds and whose axes plunge at 10°–20° west or WSW. These are common in the thrust blocks in the Ambajhiri, Deolapar and Sonawani areas.

(4) Those whose axes plunge in the direction opposite to that of earlier folds at intervals along their strike. This type is commonly seen in the southern belt of isoclinal folding, *e.g.*, in the Bharweli-Ukwa syncline in eastern Balaghat District, in the Chilhla-Mangarli region in northern Bhandara District and in the Goguldoho–Junewani–Suwardhara in northern Nagpur District.

Cross-folding is seen to be intensely developed in the central belt of gneissic formation extending from Ramtek to Pusada and Tirodi where the first type is common. A number of granite plutons is also seen along this axis indicating the severity of deformation. The intensity of cross-folding fades out on either side of this central axis, where other types of cross-folds are developed, and no granite plutons are seen.

Faults and Thrusts

Faults and thrusts occur mainly in the southern belt of isoclinal folding and northern belt of recumbent folds and thrust sheets. They include (1) steep to moderate dipping strike and reverse faults (thrusts) and (2) steep dipping transverse faults. The northern belt of thrust sheets and nappes is characterized by steep to moderate dipping folded thrust plates and low to moderate dipping thrust blocks.

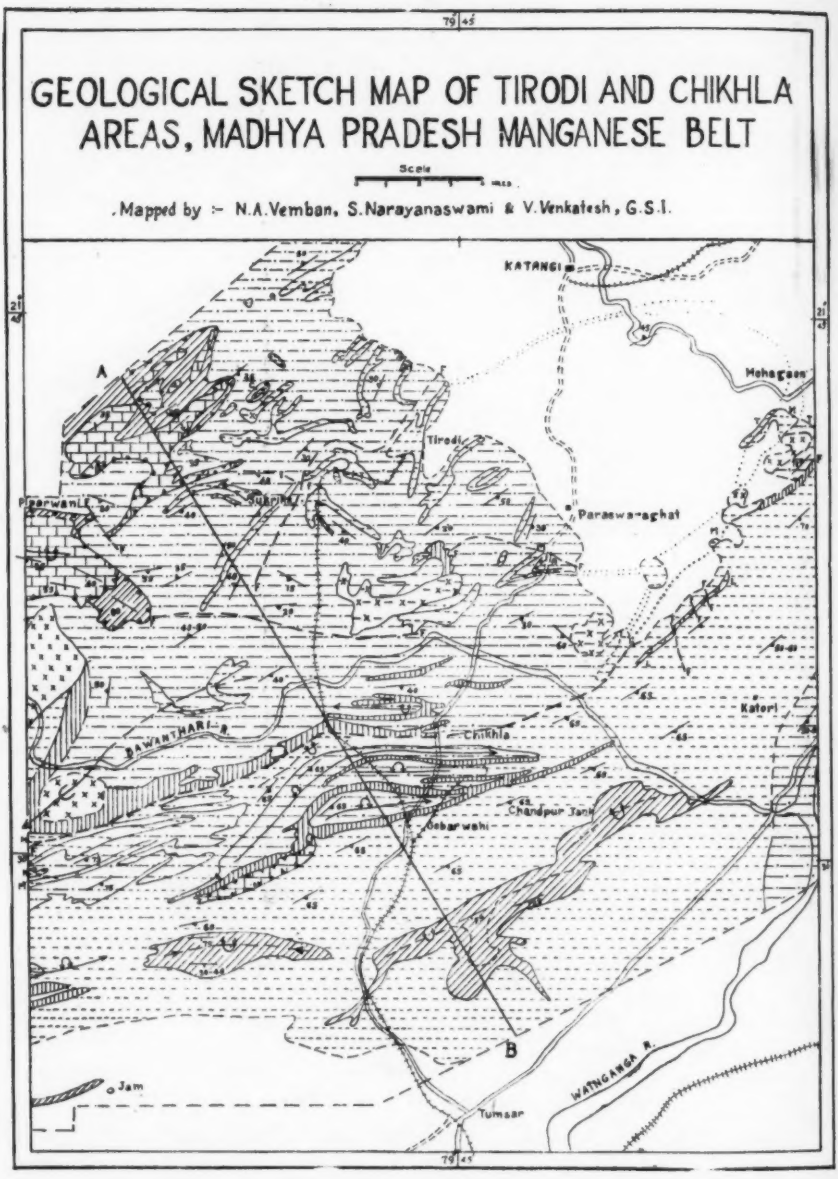

FIG. 1. Geological sketch map of Tirodi and Chikhla areas, Madhya Pradesh Manganese Belt.

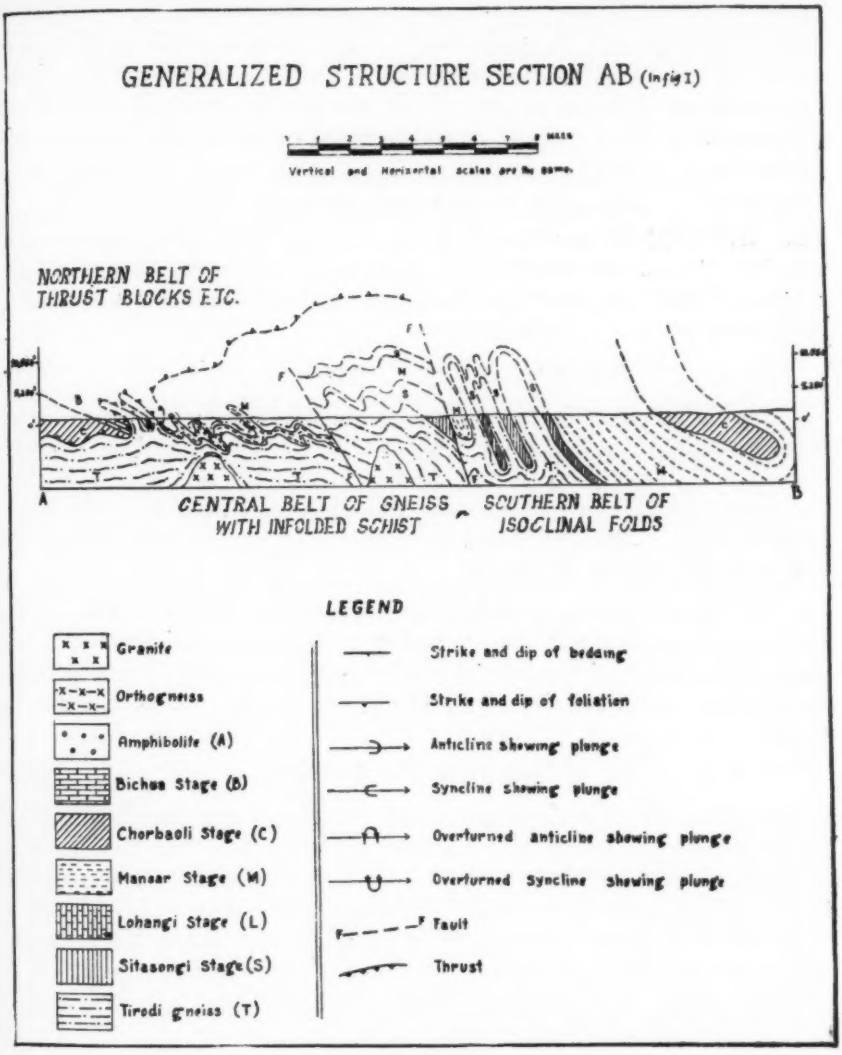

FIG. 2. Generalized structure section AB (in Fig. 1)

1. *Strike faults and thrusts.*—These faults strike generally parallel to the trend of the adjoining formations for considerable distance and at places cut obliquely across some of them. They dip generally southward in Nagpur and northern part of Bhandara Districts, and northward further

to the north-east in conformity with the dip of formations and of the fold axes. There are about a dozen faults in the manganese ore belt, some of which are traceable for over 30 miles. They have been distinguished by the occurrence of zones of silicification and epidotization, by the presence of vein quartz and pegmatite, or by structural or stratigraphic discordance.

2. *Transverse faults.*—These are minor faults whose strike varies from NNE–SSW to north-south in north–eastern Nagpur District, to north-south and NNW–SSE in northern Nagpur, northern Bhandara and Balaghat Districts. These are normal faults and occur dominantly along belts of competent beds of quartzites, calc-granulites, gneisses and gondites or manganese ore.

Age Relations of Faults and Folds

The major strike faults and thrusts show relatively small discordance between lithologic units, and are believed to have developed contemporaneously with the major period of folding. The important feature of these faults would be flowage rather than total rupture; in a belt of overturned isoclinal folds, differential shearing stress would play a major part giving rise to reverse faults or thrusts.

The minor transverse faults show limited displacements and disrupt the folds across their axial planes, and also cut across the thrust blocks and major strike faults. They are believed to be of the nature of tension faults, produced as a result of the release of stress at the close of the deformation period.

Foliation and Banding

Foliation, often in conjunction with banding, is prominently developed in these intensely folded and metamorphosed rocks. The foliation is a function of the parallel alignment of micas, of the thickness of individual layers and the proportion and size of micas. The Mansar muscovite schists show the most intense development of foliation, followed by the Junewani, Chorbaoli and Sitasongi schists and Mansar and Tirodi gneisses.

Banding due to segregation of certain groups of minerals in one layer in contrast to those in adjacent layers is common in the Lohangi and Bichua calc-gneisses, Tirodi biotite-gneiss and in the manganese ore bed, and to a lesser extent in the gneisses derived by feldspathization of Mansar, Chorbaoli and Junewani schists.

Foliation and banding throughout the manganese ore belt are generally parallel to bedding, and conform to the axial planes of the folds. Exceptions are, however, seen in the noses of plunging folds, in regions of cross-

folding, where the axes are at an angle to the axes of earlier folds, around thrust blocks or nappes and near faults, intrusive granite or ortho-gneiss contacts. Flow banding is in evidence in areas of ortho-gneisses and surrounding granite plutons.

Lineations

Lineations are well developed in most of the schistose and gneissic formations of the belt. All lineations mapped are of the nature of '*b*' lineations and fall under the group of secondary lineations of Closs (1946). The various kinds of lineations observed in the area are mineral orientation, segregation of quartz-feldspathic aggregates, orientation of quartz lenses in marbles, orientation of quartz sillimanite tabloids, stretched pebbles, grooving or rodding and axes of minor folds.

In the Nagpur District and western portions of Bhandara District, the lineations are generally 20°–30° to the ESE, east or ENE; and in northern and eastern Balaghat District, these are generally to the west, WSW and SW at low angles of 10°–20°. These lineations reflect the regional plunge of major folds. Opposing lineations at low to moderate angles ranging from 10°–30° are seen pointing to the SW, WSW, west and WNW; they seem to indicate the plunge of the late cross-folds as well as the doubly plunging nature of the earlier folds. Strong lineations of 30°–50° to the SW are observed in the intensely cross-folded belt of Susurgeh in the north-western corner of northern Bhandara District. In the Tirodi area, the lineations are generally 20°–40° to the SE, parallel to the plunge of major folds, while a few plunge at 10°–20° to the NW; the wide variation in the plunge of lineations in this area appears to be due to the complicated nature of the recumbent folding in this region.

In addition to the above, there are lineations in schists at Chikhla–Sitasongi and Netra manganese mines, which point at low angles of 5°–15° to the west or north-west, and are opposed or divergent to the axes of major folds. These are probably developed as a result of flowage folding within the troughs of tight folds. Elsewhere, wrinkles and crenulations in schists, elongation of pebbles, etc., plunge almost perpendicular to those described above. These are generally steep and could be described as '*a*' lineations, and correlated with the '*b*' lineations described.

Concluding Remarks

The sedimentary cycle that deposited the Sausar sequence in an ENE trending geosynclinal basin was followed by the Satpura orogeny which uplifted and deformed them. The deformation seems to have taken place in two stages of folding and faulting, followed by intense metamorphism

and emplacement of granite plutons. The tectonic history may be summed up as follows:

1. Folding on easterly axes resulting in isoclinal folds. The overturning of the folds to the north indicates that the predominant movements came from the south, except towards the north-eastern parts of the belt where the folds are overturned to the south by movements coming from north.

2. Increasing movements from the south or north resulting in recumbent folding, strike faulting and over-thrusting of rocks in blocks, sheets and nappes. This was followed by post-thrust strike and oblique faults and later transverse faults.

3. Recrystallization of rocks, regional metamorphism and syntectonic granitization with the formation of schists, granulites and gneisses.

4. Refolding of earlier folds on transverse to parallel axes; the axial planes are themselves refolded into isoclinal cross-folds.

5. Emplacement of late tectonic granite plutons, pegmatites and vein quartz and formation of ortho-gneisses, feldspathization, composite gneisses, etc.

6. The fold mountains of the Sausar Series were then eroded and base-levelled to a great extent, leading to the present topography.

7. The Lameta rocks represent the late Cretaceous fluviatile to lacustrine or freshwater deposits followed by outpourings of the Deccan Trap volcanic lava of late Cretaceous-Eocene age. These are essentially undisturbed, but are traversed by gravity faults.

8. The scarp topography along the Satpura range, seen north of the Katangi-Waraseoni plains, is evidence of a late Tertiary uplift.

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TECTONICS OF MYSORE STATE*

By C. S. Pichamuthu

(Singapore)

In a paper published by the writer in 1951 (*Curr. Sci.*, **20,** 117–19), the structural pattern of Mysore State was briefly described. By using as marker a prominent band of ferruginous quartzite which was manganese-bearing and often associated with limestones, it was shown that the Dharwar formations of the Shimoga and Chitaldrug Belts formed part of a big anticlinorium which plunged NNW. This was an over-simplification of the complicated tectonics which one normally expects in a Precambrian area, but it served to emphasize the fact that what were described so far in Peninsular India as separate schist belts should really be considered as stratigraphically and structurally united.

It was also pointed out that the quartzite beds were all older than the iron-manganese-limestone formation, and were found only within the limbs of the anticlinorium. This explained why the wide expanses of Dharwar Schists to the north-west of Kumsi in the Shimoga belt, and to the east of the Anaji–Janehar line in the Chitaldrug belt, were entirely devoid of quartzite beds. Stratigraphically, the quartzite beds are older than the manganiferous ferruginous quartzites, and hence occupy the centres of the anticlinal folds; a good illustration of this is furnished by the Dodguni anticline in the Tumkur District.

The writer has now prepared a structural map (Fig. 1) of a part of Mysore State which gives an idea of the main tectonic pattern of this part of the Indian Peninsula. A significant fact which emerges from this map is that the geological structure of this part of Mysore State has resulted as the consequence of folding of beds which were *already folded.* A clue to this interpretation is given by the sharp bending back of the ferruginous quartzite beds at Mertiparvata, a few miles north of Kalasa, in the Western Ghats.

The structure of the Bababudan ranges has also to be interpreted as caused by the refolding of a plunging syncline which closed eastwards, the nose having undergone concertina-like crumpling.

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* Paper presented to the Symposium on Tectonics, December 1959.

The Joldhal-Ubrani area has suffered considerably when the anticlinorium was formed. The beds of quartzites and ferruginous quartzites involved in this folding have been twisted and broken up, so that there is at present great diversity in the directions and magnitudes of their dips.

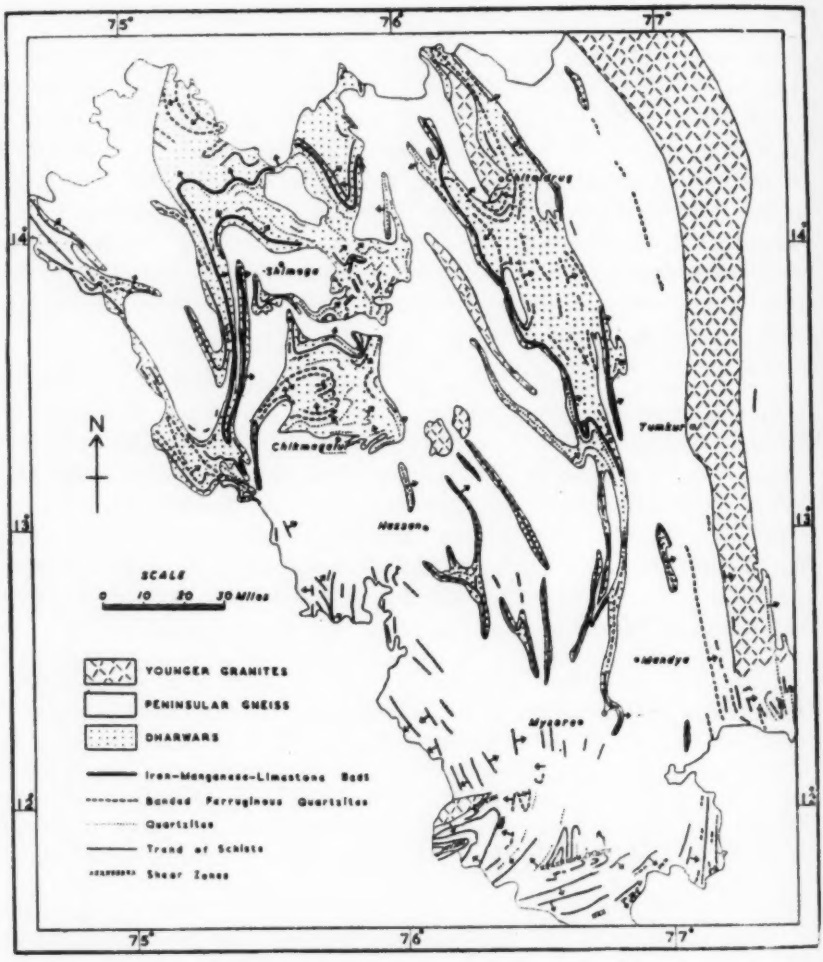

FIG. 1. Sketch map of part of Mysore State to illustrate the tectonic pattern. Only the main trends of the chief rock types are given in order to bring out the structure.

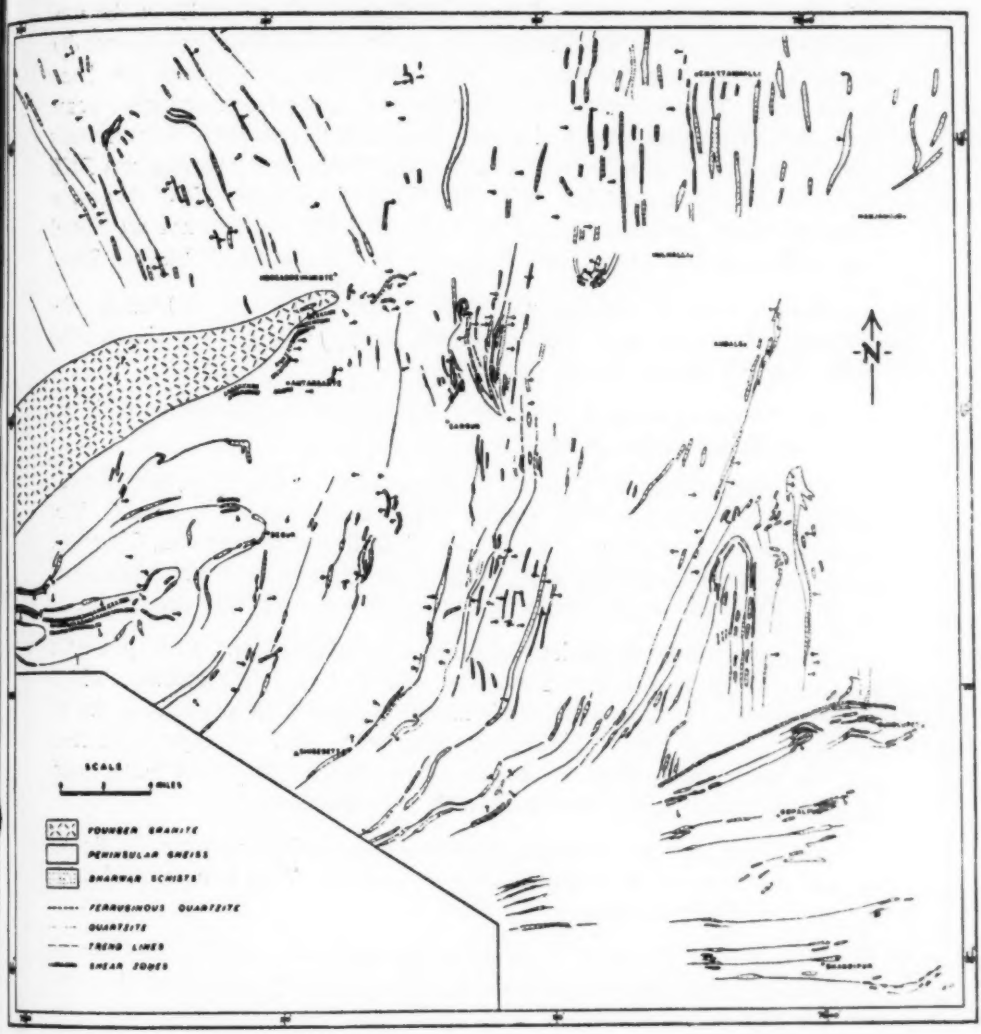

FIG. 2. Structural map of the extreme southern portion of Mysore State. The deflection of the strike directions, and the folded nature of the rock formations can be seen.

The southern part of Mysore State affords evidences of a later tectonic episode. The terrain here is extremely difficult for geological work as most of it is covered by dense forest. It is interesting, however, to note that a well-marked structural pattern does emerge from the meagre data available in this region (*vide* Fig. 2).

The general trend of the Dharwar Schists which was SSE in the west and N–S in the centre, changes first to south-west and finally to almost due west. The beds have been thrown into folds whose axial planes are themselves bent. The occurrence of mylonites and crushed gneisses gives some indication of the intensity of the disturbances in this region. A prominent shear belt can be traced for several miles near Antarsante, running in a ENE to WSW direction. A few miles WNW of Gundlupet, E–W beds are abruptly thrust against beds striking N–S. NE–SW shear zones are found also in the extreme south of the State near its boundary with Madras State.

Further south in the Nilgiri and Coimbatore Districts of Madras, the regional trend is more in accord with the abrupt change in strike noticed in this part of Mysore State.

The following tectonic episodes are envisaged in accordance with the structural interpretation proposed in this paper:

The earliest orogeny resulted in the folding of the geo-synclinal beds into a system with the axial planes disposed somewhat west-east. The folds appear to have plunged westwards. The Saulanga, Honnali, Shimoga, Jampalanaikankote, Pitlali and Bukkapatna granites and the ultrabasics of the Lakkavalli region are probably associated with this orogenesis.

This was followed not long after by a subsequent and more powerful orogeny, which folded the Dharwars into a huge anticlinorium which pitches NNW. This gave all the beds the prevailing Dharwarian strike of Peninsular India. The Chitaldrug, Hosdurga and Closepet granites, and the chromite-bearing ultrabasics of the Nuggihalli schist belt, could be considered as being associated with this orogenesis.

The third episode violently disturbed the rock formations in South Mysore resulting in twisting the beds westwards. This is connected with the Eastern Ghats orogeny.

There is an increase in the grade of metamorphism in Mysore State as one proceeds from north to south. The Dharwar schist exposures thin out considerably in South Mysore and are found only in small patches and narrow streaks. The chloritic and hornblendic schists of the north have been modified into granulites and charnockites. That we are still dealing with the Dharwars is made obvious by the occurrence of runs of such characteristic rocks as banded ferruginous quartzites, quartzites, and crystalline limestones. From Fig. 2 it can be seen that in spite of the metamorphism and the meagreness of the schist outcrops, the structural pattern can still be reasonably reconstructed.

This preliminary account of the writer's further observations on the tectonics of Mysore State is presented here for discussion and criticism.

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LIFE WITHOUT BREATHING OXYGEN—II

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Received January 16, 1961

Intravenous injection of oxygen in dogs and human beings at body temperature has been given by various observers. The amount that can be thus introduced is very small, about 25 per cent. of the total requirements in dogs and 5–6 per cent. in human beings. There are however two methods by which it has been found possible to supply all the oxygen requirements of dogs by the intravenous route. Singh (1935) found that the amount of oxygen that could be injected intravenously was increased if the atmospheric pressure, under which the experiment was performed, could be raised; he was able to keep a dog alive without breathing oxygen through the lungs for 16 minutes by injecting oxygen intravenously under 4 atmospheres of air pressure. The second method is to lower the oxygen consumption by hypothermia to such an extent that it equals the amount of oxygen that can be injected intravenously, the animal being under ordinary atmospheric pressure (Singh, 1960); this was done by lowering the body temperature of dogs to 20–20°C. In further experiments (Singh, Singh and Singh, 1960), it was found that the best temperature for intravenous injection of oxygen was 25–27° C.; in the present research, therefore, an attempt has been made to keep dogs alive without breathing oxygen at 25–27° C.

Methods

The chief difficulty in these experiments is the increased oxygen consumption due to shivering. This has to be prevented by injection of tubocurarine. Seven unselected mongrel dogs, varying in weight from 15 to 20 kg. were used. A preliminary injection of atropine sulphate, gr. 1/100, was given subcutaneously. Basal narcosis was induced by intraperiotoneal injection of 30 mg./kg. pentobarbitone, to reduce shivering; anæsthesia may be deepened, as such a procedure diminishes shivering. When the dogs came under the anæsthetic, a tracheal cannula was inserted and artificial respiration started with an Ideal respiration pump, which was connected to a Benedict-Roth apparatus to measure the oxygen consumption. An injection of tubocurarine (15–30 mg.) was then given intravenously. The body temperature was reduced at the rate of 1° C. in 10 minutes by surface cooling with ice to 25–27° C.

Oxygen was injected from a cylinder by means of a side tube connected with a cannula. The cannula was attached to a burette filled with normal saline and was tied to a small vein of the foot. The incjection was made by two 50 c.c. Record syringes which filled and emptied alternately. Electrocardiograms were recorded frequently to know the condition of the heart.

The begin with, the spirometer tracings rise at an angle which is proportional to the oxygen consumption. The dog may be considered not breathing oxygen from the exterior if during intravenous injection of oxygen these tracings become horizontal, the heart beating normally as shown by the electrocardiogram.

Results

The results are shown in Table I. It was possible to keep all the 7 dogs alive without breathing oxygen from 15 to 25 minutes (Fig. 1).

Table I

Intravenous injection of oxygen in dogs at 26° C. rectal temperature

Number of experiment	Weight of dog, kg.	Oxygen consumption at 26° C., c.c. per min.	Intravenous injection of oxygen, c.c. per min.	Total oxygen injected, c.c.	Minutes kept alive without breathing oxygen
1	18	41	40	1000	25
2	16	32	30	600	20
3	16	40	40	600	15
4	20	52	50	1000	20
5	17	42	40	800	20
6	18	50	50	1000	20
7	16	30	30	600	20

Discussion

Intravenous injection of oxygen at 25–27° C. has been found to be the most convenient and easy method to demonstrate life without breathing oxygen through the lungs in dogs. All the oxygen required by the animal

can be supplied by the intravenous route so that they need not breathe oxygen from outside.

SUMMARY

If the body temperature of dogs is reduced to 25–27° C., it is possible to give all the oxygen required by the animal by the intravenous route so that they need not breathe oxygen from outside.

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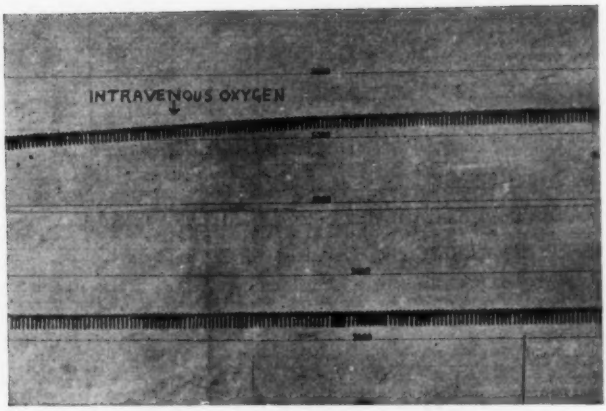

FIG. 1. Intravenous injection of oxygen in dog at rectal temperature 26° C. Respiratory tracings. At arrow mark oxygen injected at the rate of 40 c.c. per min. The tracings become horizontal after about 2 min. This lag is due to the dead space between the Benedict-Roth apparatus and the dog. Lower tracing continuation of the upper. Weight of dog, 17 kg.; oxygen consumption, 42 c.c. per min.

EFFECT OF AGE, SEX AND GONADAL HORMONE ON BRAIN TISSUE RESPIRATION OF ALBINO RATS*

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Received September 12, 1960

Introduction

Metabolic studies in various tissues of animals have been extensively carried out by many workers (Horecker, 1955; Russel, 1951). Physiologically the brain is the controlling and directing centre of the body.

Oxidative glucose metabolism is the primary and indispensable source of energy for brain tissue. It continuously resynthesises energy-rich phosphate compounds in the brain. It is supposed that normal functions are uniquely dependent on an uninterrupted and ample supply of oxygen. It has been shown by many workers that if the cerebral delivery of oxygen is arrested by stopping the cerebral circulation, consciousness is lost in a few seconds. The activities of most of the tissues in the body are altered with age and the change is likely to be related to sex hormones. It was, therefore, decided to make a study of brain tissue metabolism in order to see the influence of age, sex and gonadal hormone on its overall respiration.

Material and Methods

Male and female albino rats of local variety were used throughout the study. The animals were divided into various groups as given in Table I. The rats were decapitated at the time of experiments. QO_2 of the brain was determined by the direct method of Warburg. The oxygen consumption of the brain slices respiring in Krebs Ringer Phosphate Solution (pH 7·2) carrying 2% glucose was measured at 38° C. for 1 hour. Brain slices were cut free-hand with a good safety razor blade. The tissue was excised immediately after the animal was killed and kept at a refrigeration temperature for 2-3 minutes. Slices were then taken, without delay, by chopping. Slices 100 mg. by wet weight were used for the experiment. At the same time 100 mg. by wet weight of tissue slices were kept for the estimation of its dry

* Part of the work submitted for the M.Sc. Thesis of the Bombay University in 1960

weight. The gas phase was atmospheric air. The reaction was carried out at a shaking rate of 55 oscillations per minute.

TABLE I

Groups of rats used

Group I	..	New-born rats, 10–15 days old.
Group II_M	..	Male rats, weighing between 55 and 95 gm.
Group III_M	..	Male rats, weighing between 120 and 150 gm.
Group IV_M	..	Male rats, weighing over 200 gm.
Group II_F	..	Female rats, weighing between 55–95 gm.
Group III_F	..	Female rats, weighing between 120 and 150 gm.
Group IV_F	..	Female rats, weighing over 200 gm.
Group V_F	..	Female rats, kept as a control over group VI_F.
Group VI_F	..	Female rats, ovariectomised one month previously (initial weight between 50 and 60 gm.)
Group VII_F	..	Female rats, ovariectomised as in Group VI_F and treated with subcutaneous estradiol benzoate 0·5 mg. per day for terminal seven days.

RESULTS AND DISCUSSION

The results are summarised in Tables II, III and IV. It will be seen that there is a rise in oxygen uptake as the weight of the rat increases except in the new born animal where the oxygen uptake is related to dry weight only. However, if the oxygen uptake is calculated on the basis of wet weight then it is found to be lower than in the animals of the next higher age (body weight) group. This difference is probably due to a markedly higher water content of the brain tissue of the new born as compared to that of older animals. In the present study it was observed that whereas in the new born tissue water constituted as much as about 90% of the total wet weight and that in the older group was about 80% only. The value reaches to the maximum when the body weight reaches 150 gm. Then there is a definite fall in the oxygen consumption of the tissue.

Different levels of metabolism can be distinguished in the animals during post-natal life. The metabolism during first 15–20 days of life is characterised by a low oxygen and glucose utilisation. At the age of 10–12 weeks (*i.e.*, when body wight is about 150 gm.) the respiration is highest. The adult level is obtained after about 22–24 weeks (*i.e.*, when body weight of rat is over 200 gm.).

TABLE II

Brain tissue respiration in different groups of male and female rats

Group No.	No. of animals	Body wt. gm.±σm.*	Mean QO_2: µl. of O_2 uptake/100 mg. wet wt./hr.±σm.*	Mean QO_2: µl. O_2 uptake/mg. dry wt./hr.±σm.*
I	6	16·05±1·13	57·27±1·85	4·37±0·17
II_M	6	74·9±4·57	58·44±1·98	2·79±0·02
III_M	6	137·3±4·67	98·28±3·48	4·74±0·156
IV_M	6	217 ±4·67	46·28±2·63	2·29±0·112
II_F	6	72 ±3·01	45·70±2·47	2·3 ±0·154
III_F	6	130 ±3·62	64·8±3·15	2·82±0·056
IV_F	6	225 ±8·11	38·89±1·16	1·80±0·0113

* σm. = Standard deviation of the mean.

Respiratory metabolism of rat brain tissue by slice technique has been studied by many authors (Elliott, 1955; Greengard and McIlwain, 1955). The variation in the values obtained in the present study may be due to the differences in the details of the technique used. Thus we used lower speed of oscillation in the Warburg apparatus (55 oscillations/minute) and used atmospheric air as the gas phase. The variations are certainly too high to be due to difference of strain of the animals.

Koch and Koch (1913) studied the respiratory metabolism of different ages of animals. They conclude that rise in rat brain metabolism coincided with the beginning of myelinisation. They also state that the process continues with great intensity until about 4–7 weeks of life. It is also assumed that the energy required for myelinisation and many other changes occurring during the first month of life result in the high metabolisms found during

this period. Himwich and Fazekas (1941) studied the respiration of different parts of dog brain in relation to age of the animal. They reported that the high values for respiration were related to the particular part of the tissue which has started functioning. Tayler and Harreveld (1942) also obtained curves of the oxygen consumption of various parts of the developing rat brain which resembled curves reported for dog by Himwich and Fazekas.

TABLE III

Brain tissue respiration values in three groups of female rats

Group No.	No. of animals	Body weight gm. $\pm\sigma$m.*	Wt. of brain mg. $\pm\sigma$m.*	Wt. of brain per 100 gm. body weight mg.	Mean QO_2: μl. of O_2 uptake/mg. dry wt./hr./ $\pm\sigma$m.*
V_1 (Control)	6	98·6±0·070	1615±16·76	1646·3	2·62±0·013
VI_1 (Castrated)	6	125·2±6·71	1471±20·41	1183·2	3·74±0·022
VII_1 (Castrated and treated)	6	105·7±6·62	1267±21·76	1208·8	3·13±0·007

* σm. = Standard deviation of the mean.

The studies of the biochemistry of the brain during early life are limited and very few references are available concerning the relationship between biochemical and functional changes. According to some these events are related to the results of the process of myelinisation (Sp rry and Welsch, 1960). Myelinisation, from a physical point of view, is the most conspicuous change in the developing brain.

It seems likely, therefore, that the change in the values of respiration is the reflection of the fuctional activity of the brain.

Donaldson and Hatai (1931) explain that the low oxygen uptake of the infant brain involves the respiratory enzymes concerned in these processes. In the adult brain there is a greater proportion of grey (protein) and white (lipoid) matter. The greater rate of adult brain, therefore, may be correlated with the larger protein contents of the cells.

While studying the effect of sex on brain tissue respiration, it is obser ed that the values obtained for male rats are higher than those for the females.

TABLE IV

Oxygen uptake of rat brain tissue

GROUP No. I (New Born)

Expt. No.	Body weight in gm.	Dry weight in mg.	Flask No.	Actual uptake in mm.	QO_2 (wet wt.) basis	QO_2 (dry wt.) basis
1	13·0	14·0	24	−70	65·01	4·6
2	12·0	16·0	24	−61	56·65	3·54
3	18·5	13·3	24	−64	59·44	4·57
4	18·5	11·0	24	−55	51·08	4·64
5	17·3	12·0	24	−55	51·08	4·24
6	17·0	13·0	24	−65	60·37	4·64

The study of brain tissue respiration dealing with the factor of gonadal hormone shows that the brain of the castrated female rat has an oxygen uptake 35% higher than of normal rat kept as a control. The brain of castrated female rat treated with estradiol respires at a rate slightly higher than the normal which shows that it has a tendency towards normal value. It may therefore be suggested that female gonadal hormone has an inhibitory action on oxygen uptake. A possible interpretation is that the inhibiting effect of estrogen is decreased after castration and can be prevented for the most part by the administration of estradiol. This also may explain for the higher values in case of male rats than the females of equal weights.

SUMMARY

Effects of age, sex and female gonadal hormone on brain respiration in rats are studied. Oxygen consumption of the entire brain of rat rises as the weight of animal increases. It is maximum when the body weight reaches about 150 gm. Then there is a decrease in oxygen consumption. Female sex hormone seems to have an inhibitory action on the brain respiration.

ACKNOWLEDGEMENTS

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METABOLISM OF THIOSTERS OF CARCINOGENIC HYDROCARBONS

Part I. Metabolism of Dibenzothiophene

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Ever since the realisation that a chemical entity, 1 : 2 : 5 : 6-dibenzanthracene, produces cancer,[1] the compound and its structural analogues are being exhaustively studied for their chemical and physical properties, carcinogenic activity and metabolism with a view to elucidating the mechanism of carcinogenesis by hydrocarbons. Accumulated evidence of such studies led to the suggestion[2, 3] that presence of an "activated phenanthrene bridge" (9 : 10-positions in phenanthrene which are also referred to as the 'K-region') in polycylic hydrocarbons was the preponderent cause, if not the only one of their carcinogenic activity. In order to examine the validity of the above suggestion, Robinson[4] put forward an idea of synthesising certain thiophene isosters (thiosters) of carcinogenic hydrocarbons in which the phenanthrene bridge or bridges have been replaced by an isosteric thiophene nucleus as illustrated by compound (I), the thioster of the highly carcinogenic hydrocarbon, 9 : 10-dimethyl-1 : 2-benzanthracene.

Since then, thiosters of carcinogenic hydrocarbons, compound (I) and several others such as (II), (III) and (IV) have been synthesised by one of us.[5] Compounds (I) and (II) have been found to be non-carcinogenic[6, 7] by subcutaneous injection in mice, but when painted on the skin the former compound has been found to possess a weak carcinogenic activity. Compound (III) is a strong carcinogen[6] even more potent than its hydrocarbon analogue. Compound (IV) is also carcinogenic.[6] The behaviour of the compounds (III) and (IV) indicated that they were apparent exceptions to the activated phenanthrene bridge hypothesis.

A careful analysis of the available data on the carcinogenicity of hydrocarbons and their thiosters suggested that as regards carcinogenicity there

may not exist direct interrelationship between hydrocarbons and their corresponding thiosters. It seemed likely that the sulphur atom in the condensed thiophene has its own characteristic reactivity towards a biological substrate. Although a di-univalent sulphur in a heterocyclic aromatic system is electronically equivalent to a conjugated double bond in aromatics, nevertheless the sulphur atom might impart a distinctive chemical reactivity to the molecule. Thus, the sulphur atom may undergo oxidation to a sulphoxide or sulphone

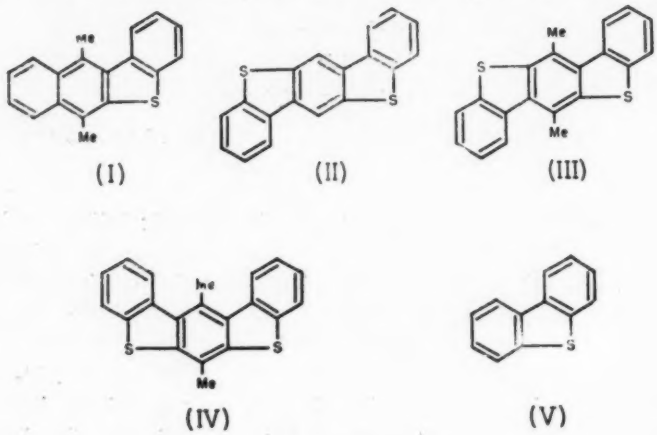

CHART I

grouping and/or it may induce facile substitution in rest of the molecule. In order to find out whether the sulphur atom in condensed thiophenes is involved in metabolism or not, metabolic studies of certain condensed thiophenes were deemed essential. Among the condensed thiophenes, thionaphthene alone has been studied for its metabolism[8] in rabbits and a thionaphthene-alpha-glucuronic acid of undetermined constitution has been reported to have been isolated from their urine. The present paper deals with the metabolism of dibenzothiophene (V) (referred to hereafter as DBT) in rats. DBT was selected for the preliminary study of the metabolism of thiosters since most of the thiosters that have been tested for carcinogenicity contain DBT as a structural unit.

DBT was incorporated in diet and fed to male rats of Wistar strain. The animals were kept in metabolic cages equipped with an arrangement for collection of urine. Pooled samples of urine were acidified to congo-red (pH 3–5), hydrolysed and extracted with ether. The ethereal extract was shaken with sodium hydroxide solution and the alkaline solution, on acidifi-

cation yielded a solid, which on crystallization gave a compound (VI), m.p. 258–59°. It formed acetyl (m.p. 210°), benzoyl (m.p. 206–07°) and O-methyl (m.p. 208–11°) derivatives.

Elementary analysis of the metabolite (VI), its derivatives and its infra-red spectrum (two, high intensity bands a 1150 cm.$^{-1}$ and 1295 cm.$^{-1}$ characteristic of the sulphone group and a s rong band at 1200 cm.$^{-1}$ characteristic of the phenolic hydroxyl group, *see* Fig. 1), showed that it is a hydroxydibenzothiophene-5: 5-dioxide. Since it is known[9] that sulphoxides exhibit a strong band in the range 1060-1040- cm.$^{-1}$ in solution with a corresponding reduction of 10-20 cm.$^{-1}$ in the solid state, while sulphones exhibit two bands: the first in the narrow range 1160–1140 cm.$^{-1}$ and the second in the range 1350–1300 cm.$^{-1}$ in solution, with only slight shifts in the solid state.

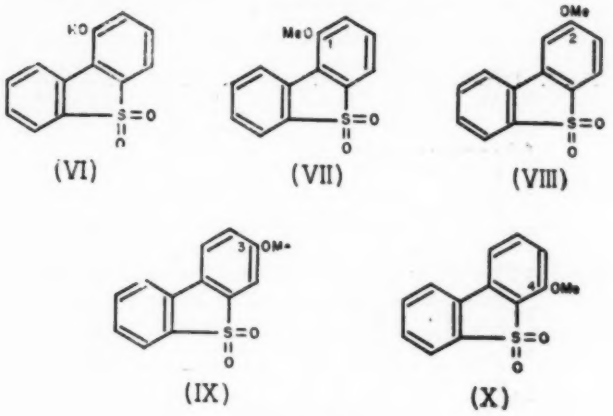

CHART II

The O-methoxy derivative (m.p. 208–11°) of the metabolite (VI) was different from 2-methoxydibenzothiophene-5: 5-dioxide (m.p. 244°, VIII) 3-methoxydibenzothiophene-5: 5-dioxide (m.p. 218–20°, IX), and 4-methoxydibenzothiophene-5: 5-dioxide (m.p. 191–92°, X). The latter compounds have been prepared by us unambiguously and will be reported in a separate communication. The ultra-violet spectra of the O-methyl derivative of the metabolite (VI) and of the compounds (VIII, IX and X) are shown in Fig. 2. The metabolite (VI) is, therefore, 1-hydroxydibenzothiophene-5: 5-dioxide (VI).

The aqueous layer of the hydrolysed urine remaining after extraction with ether was made alkaline (pH 10·0) with sodium hydroxide solution. The alkaline urine showed the presence of dibenzothiophene-sulphonic

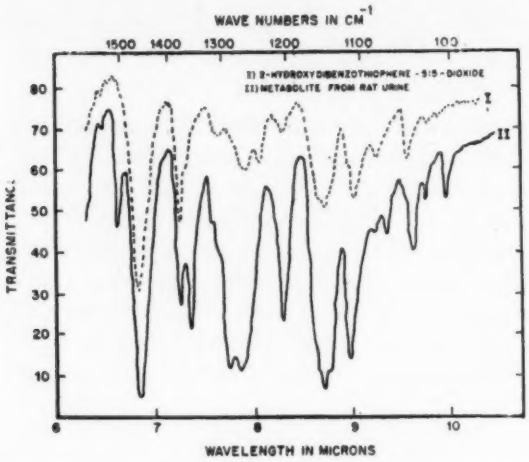
WAVE NUMBERS IN CM⁻¹
1500 1400 1300 1200 1100 100
I) 2-HYDROXYDIBENZOTHIOPHENE - 5:5 - DIOXIDE
II) METABOLITE FROM RAT URINE
I
II
TRANSMITTANC.
80 70 60 50 40 30 20 10
6 7 8 9 10
WAVELENGTH IN MICRONS

FIG. 1. Infra-Red Spectra of compounds (I) and (II) in Nujol-Mull.

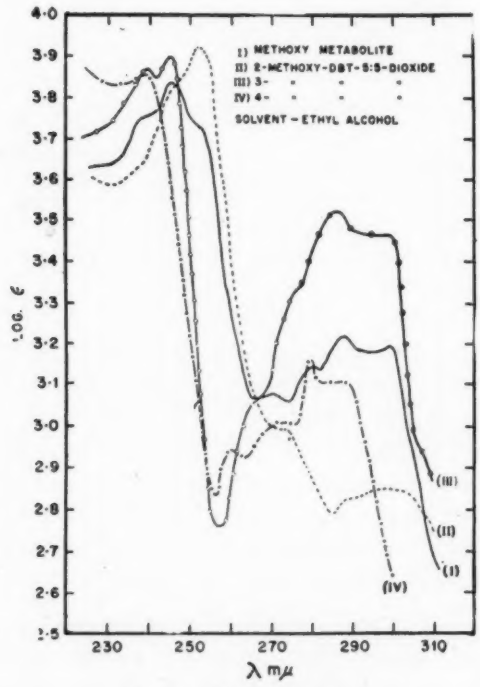

FIG. 2. Ultra-violet Spectra.

acid, as evidenced by the formation of crystalline salts with aniline hydrochloride and *p*-chloraniline hydrochloride. It seems likely that DBT is also metabolised as a water-soluble sulphonic acid derivative.

The normal metabolism of hydrocarbons in rats and mice leads to α-hydroxy derivatives[10] and an introduction of the hydroxyl group is assumed to occur through the mechanism of perhydroxylation. The metabolism of DBT in rats also resulted in hydroxylation of the molecule in the 1-position and in addition, oxidation of the di-univalent sulphur atom in (V) to the sulphone group has taken place leading to the metabolic elution of DBT (V) as 1-hydroxydibenzothiophene-5 : 5-dioxide and a water-soluble sulphonic acid derivative.

In view of Heidelberger's observations[11] that 1 : 2 : 5 : 6-dibenzanthracene is conjugated with proteins *in vivo* at the K-region and metabolized as 2-phenylphenanthrene-3 : 2′-dicarboxylic acid, and our present finding that, the sulphur atom in DBT which isosterically substitutes the K-region is also oxidised *in vivo*; it may be concluded that the K-region is not immobilized as regards carcinogenicity in thiosters since the sulphur atom, like the K-region is also implicated in an oxidative process. The present study, therefore, explains the apparently anomalous behaviour of the key thiosters such as (I), (III) and (IV) as regards their carcinogenic activity.

In conclusion, DBT is metabolized through hydroxylation in the 1-position and is oxidised at the chemically reactive sulphur atom in the molecule. These changes are such as might be expected to interfere with the oxidative mechanism of the cell.

Experimental

Preparation of Dibenzothiophene.—Dibenzothiophene required for the metabolic studies was prepared according to the method of Gilman and Jacoby.[12] The product was purified by distillation under reduced pressure and by crystallisation from ethyl alcohol, when it yielded colourless needles m.p. 99°. Yield 35%.

Metabolic Study of DBT.—A batch of 12–24 young male rats (1½–2, months) of Wistar Strain was used. The animals were kept in four to eight metabolic cages which were provided with an arrangement for collecting urine. The animals were maintained on a colony diet,* incorporating 0·25%

* Composition: Wheat 66, Gram-flour 15, Fish meal 7, Yeast 5, Groundnut 5, Shark-liver oil 1, and Sweet oil 1%. When DBT was incorporated in the diet, corresponding amount of wheat was reduced.

DBT and water *ad. libitum*. Weekly weights of the animals were recorded and these were found to be of the same order as those of animals on normal diet.

The daily output of urine of one rat, dosed with DBT, was about 1·50 to 3·0 c.c. The urine was pooled and preserved over copper sulphate crystals in a refrigerator. The collection of 3–4 months urine was worked up at a time.

Isolation of 1*-hydroxy-dibenzothiophene-*5: 5*-dioxide* (*VI*) *from rat urine.*—Urine (500 c.c.) was filtered, acidified with concentrated hydrochloric acid to congo-red and boiled for 30 minutes. The hydrolysed urine was cooled and extracted with peroxide-free ether (5×100 c.c.). The concentrated ethereal extract (100 c.c.) was exhaustively shaken with 1 N. sodium hydroxide solution (5×20 c.c.). The alkali-soluble fraction (*a*) separated, and it was worked up as described in the succeeding paragraph. The urine layer was further worked up.

The alkali-soluble fraction (*a*) was acidified with concentrated hydrochloric acid (congo-red) and the solution extracted with peroxide-free ether (5×100 c.c.). The ethereal extract yielded 1-hydroxydibenzothiophene-5: 5-dioxide (VI), which, on several crystallisations from water, gave clusters of colourless, shining needles, m.p. 258–59° (Found: C, 62·0; H, 3·7. $C_{12}H_8O_3S$ requires C, 62·0; H, 3·5%). Yield of the crude product was about 50 mg. from 2 litres of urine.

Properties of the compound (*VI*).—It was soluble in ethyl alcohol. It was insoluble in 5% sodium bicarbonate solution. An aqueous solution of (VI) did not give any colouration with ferric chloride solution.

Acetate of compound (*VI*).—The compound (0·02 g.) was refluxed with acetic anhydride (2·0 c.c.) and pyridine (2–3 drops) for one hour. The mixture was cooled, diluted with water and kept in the refrigerator. The acetate was filtered and washed with (i) 20% hydrochloric acid, (ii) 5% sodium hydroxide solution and finally with distilled water. The acetate crystallised from ethyl alcohol in plates (0·012 g. Yield 60%), m.p. 210°. (Found: C, 61·2; H, 3·88, $C_{12}H_7O_3S + COCH_3$ required C, 61·32; H, 3·68%).

Benzoate of compound (*VI*).—Compound (VI) (0·014 g.), benzoyl chloride (0·1 c.c.) and pyridine (2·0 c.c.) were refluxed on a water-bath for two hours. The reaction mixture was cooled and hydrochloric acid (10 c.c. 5 N) added to it. The solution was then extracted with peroxide-free ether and the ethereal extract was successively washed with 2% NaOH, 2% HCl and 2% $NaHCO_3$ solutions. The product obtained from ether extract crystallized

from dilute ethyl alcohol in needles (0·007 g. Yield 50%) m.p. 206–07°. (Found: C, 67·9; H, 3·4. $C_{19}H_{12}O_4S$ requires C, 67·85; H, 3·6%).

Methyl ether of compound (VI).—Compound (VI) (0·02 g.) was dissolved in anhydrous acetone (5 c.c.). To the solution, freshly ignited potassium carbonate (0·14 g.) and dimethyl sulphate (0·05 c.c.) were added and the mixture refluxed for 8 hours. After cooling, the reaction mixture was filtered and the residue washed with acetone. The product from acetone extract was then extracted with peroxide-free ether. The ether extract was washed with 5% NaOH (2×20 c.c.). Removal of ether gave the methoxy derivative, which crystallized from aqueous ethanol, in colourless long rectangular plates, (0·016 g. Yield, 66%) m.p. 208–11°. (Found C, 63·5; H, 4·7. $C_{13}H_{10}O_3S$ requires C, 63·41; H, 4·1%).

Formation of arylamine salts with the urinary sulphonic acid.—The urine layer remaining after the separation of compound (VI) was made alkaline to pH 10·0 with 10% sodium hydroxide solution. The alkaline urine was evaporated to dryness on a steam-bath. The product was dissolved in water to give a 50% solution. A portion (2 c.c.) of the solution was boiled separately with two different arylamine hydrochlorides. The resulting solutions, on cooling, gave colourless crystalline salts: (*a*) the salt with anilinehydrochloride melting at 158–61° and (*b*) the salt with *p*-chloraniline hydrochloride which melted at 150–51° (decomp.).

Summary

Dibenzothiophene (DBT) when given to rats is eliminated through urine as 1-hydroxydibenzothiophene-5: 5-dioxide and an unidentified sulphonic acid. DBT is thus metabolised in a manner similar to 1: 2: 5: 6-dibenzanthracene. Since, the sulphur atom in the thiosters, like the 'K-region' in 1: 2: 5: 6-dibenzanthracene, is implicated in an oxidative process, the 'K-region' is not immobilized as regards carcinogenicity in the thiosters. The present work explains the carcinogenic activity of the key thiosters observed by earlier workers.

Acknowledgements

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THE CHEMICAL COMPOSITION OF THE DIATOM FRUSTULE

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Introduction

It is well known that the frustule or the wall of diatoms is siliceous. But the exact chemical composition and the physical condition of the silicate present is not quite clearly known at the present time.

Kützing (1844), Ehrenberg (1834), Bailey (1856) and Weiss (1871) found that SiO_2 was present in the frustule, and for a long time it was thought that SiO_2 was the only constituent. Subsequently definite evidence has been obtained that SiO_2 constituted up to as much as 87–99% of the ash, and that a smaller portion (up to 2%) was made up of ferrous and aluminium oxides. Some other elements are also found in traces [*see* for instance Kützing (1844), Samoilov and Roskhova (1925), Rogall (1939), Vinogradov (1953), Desikachary (1956), also Murray and Penard (1891), Kützing (*ex* Ehrenberg, 1834), Naumann (1930), Richter (1911), Sjostedt (1921) and Tschirwinsky in Novotscherkesk (1925)]. Estimations have shown that the SiO_2 content varies with the individual species and with the environmental conditions in which they grow [Pia (1926), Rogall (1939), Einsele and Grim (1938)]. The centric diatoms as a rule are found to have a lesser quantity of silica than the pennate forms.

The silica in the diatom frustule is considered, in recent times, as amorphous [Kahane (1935), Rogall (1939), Vinogradov (1939)]. According to Liebisch (1929–30) the silicate in the frustule is in the form of hydrated silica $SiO_2.xH_2O$ very similar to opal; while Cooper (1952) is of the opinion that the chemical constitution of the diatom skeletons is similar to that of hydrated silica dispersed in water. Rogall (1939) concluded from his studies that the frustules were made of pure silicic acid in a sub-colloidal state. The

difficulty arises in correlating the above observations on the present-day diatoms with that of the crystalline condition of the silica seen in the fossil diatoms [Rogall (1939) and Geissler (1958)]. There are two ways of explaining this. It is possible that in both the recent and the fossil diatoms silica is present in a crystalline condition, but that the crystalline pattern is obscured by the diffuse diffraction pattern due to other material such as protein or pectins in the present-day diatoms. The other explanation is that the deposition is in an amorphous condition and that only during fossilization there is a rearrangement of the molecules leading to a progressive crystallisation of the silica. In other words, the latter assumes that the silica is transformed during fossilization of the diatoms from an amorphous to a crystalline condition.

The fact that the silica in the present-day diatoms is in an amorphous condition was deduced by the earlier workers from their isotropic behaviour since they are optically non-birefringent and also because there is a negative membrane potential. The absence of any distinguishable crystalline pattern in diffraction studies also confirmed this idea. The fossil diatoms on the other hand yield a diffraction pattern characteristic of a crystalline condition, and have a much lower membrane potential than the present day diatoms (Geissler, 1958).

These X-ray diffraction studies on the diatom frustules were carried out by Rogall (1939) who seems to be the only one to have made such studies of the silica frustule in any detail (*see* also Kahane, 1935; Vinogradov, 1939). He found that the diatom frustule was made of pure silicic acid in a sub-colloidal condition, giving only a diffuse pattern without any powder rings characteristic of silica. In the fossil state the diatoms have an opal-like structure. The present X-ray studies on diatom frustules have yielded results which are different from those of Rogall, and indicate that the silica present in the frustule contains crystalline α-quartz as a component.

MATERIALS AND METHODS

The following materials were investigated: (1) *Isthmia nervosa* growing on red alga in pure formation, near San Francisco, California, U.S.A., which were collected during 1954 and preserved as an air dried sample. (2) A mixture of *Cyclotella meneghiniana* and *Gomphonema parvulum* (3) *Fragilaria brevistriata*. The specimens of (2) and (3) were collected from some water tubs in the Botany Department, University of Madras. (4) Fossil diatoms were obtained from deposits found at Lampoc in California, Florida in the U.S.A., and Lake Sumner and Oomaru in New Zealand.

X-ray studies were made with a ' Unicorn ' rotation camera. The radius of the cylindrical camera was 3 cm.; while the X-ray radiation used was Ni-filtered Cu Kα radiation with wavelength 1·542 Å. The diameter of the X-ray collimator used was 0·5 mm.

Suitably cleared material of *Isthmia nervosa* diatoms were also studied with a ' Norelco ' Philips microcamera, with the distance between the specimen and film equal to 1·76 cm. This distance was obtained by calibrating the camera with NaCl powder. The diameter of the X-ray collimator of the microcamera was 0·004" and one single diatom frustule of *Isthmia nervosa* cleaned with potassium dichromate and sulphuric acid was adjusted to be in the X-ray beam.

Results

1. *Isthmia nervosa.*—Untreated air-dried material (Fig. 1) as well as material preserved in rectified spirit (Fig. 2) did not give any prominent X-ray diffraction powder rings but only diffuse halos. Blackening, due to low angle scatter, up to about 8·8 Å was recorded, while two diffuse halos of spacing 4·10 Å and 2·09 Å were also present. These were similar to the halos obtained with silica gel when untreated (Fig. 3) as well as with silica gel when treated with potassium dichromate and sulphuric acid (Fig. 3 *a*). However, on repeated cleaning with potassium dichromate and sulphuric acid these diatoms gave a powder ring pattern, the most prominent rings having Bragg spacings of 3·36 Å, 2·51 Å and 1·832 Å (Fig. 5). This same material when studied in the microcamera showed prominent rings at 3·35 Å, and 4·26 Å (Fig. 6). For the complete X-ray analysis data *see* Table I.

2. *Cyclotella meneghiniana and Gomphonema parvulum mixture.*—This collection when cleaned and studied, yielded crystalline powder patterns (Figs. 7, 8 and 9) with the most prominent powder rings having '*d*' spacings of 3·35 Å, 4·43 Å and 1·820 Å (*see* Table I). The powder ring system in every case was due to α-quartz. The X-ray powder pattern of pure α-quartz is shown in Fig. 11 for comparison.

3. *Fragilaria brevistriata.*—These diatoms also gave a similar powder ring system with prominent '*d*' spacings of 3·36 Å, 4·37 Å and 1·809 Å. Here again the powder ring system is due to α-quartz. The diffraction pattern given by these diatoms is shown in Fig. 10.

4. *Fossil diatoms.*—Fossil diatoms from Florida and Lampoc in the U.S.A., and Oomaru and Lake Sumner in New Zealand yielded crystalline powder diffraction patterns with the most intense rings having spacings of 3·35 Å, 4·28 Å, 1·820 Å and 4·35 Å (*see* Table I). Bragg spacings for

TABLE I

Bragg spacings in Å *for various diatom specimens*

Present-day specimens						Fossils			α-Quartz (from A.S.T.M. Index)		Pectin	B.D.H. silica gel.	Fe_3O_4	
Cyclotella meneghiniana and *Gomphonema parvulum* mixtures	*Fragilaria brevistriata*	*Isthmia nervosa*			Lampoc (in U.S.A.)	Oomaru and Florida (same values)	Lake Sumner, New Zealand	'd' in Å	Intensity	'd' in Å	'd' in Å	'd' in Å	Intensity
		Air-dried powder specimen	Specimens after cleaning	Micro-camera results									
10·05 w	..	..	Blackening up to 8·8 Å	..	..	..	..	10·05 w	..	..	10·05 vvw	Blackening upto 8·50	..	..
..	..	7·36 w	..	..	..	..	..	7·03 w	..	..	7·03 m	..	..	..
..	..	..	..	..	..	..	..	58·1 vvw	..	..	..	..	..	..
..	..	..	..	4·94 w	..	..	..	..	..	..	..	..	4·86	30
4·43 m	4·35 m	4·37 m	4·10*	4·10*	4·26 s	4·28 s	4·27	4·35 s	4·26	35	4·43 s	4·05*	..	..
3·73 w	3·73 m	..	..	..	..	3·73 w	3·75	3·70 w	..	..	3·89 m	..	..	..
3·35 s	3·35 s	3·36 s	..	3·36	3·35 vs	3·35 vs	3·35	3·35 vs	3·343	100	3·48 w	..	..	..
..	..	..	..	..	3·12 w	..	..	..	..	..	3·14 m	..	2·97	60
2·91 w	2·94 w	2·90 w	..	..	..	..	2·94	2·91 vw	..	..	2·88 w	..	..	..
2·57 m	2·56 m	2·56 m	..	2·54	..	..	..	2·57 m	..	..	2·50 m	..	2·53	100
..	..	..	..	..	..	2·44 w	2·44	2·44 mw	2·458	12	..	..	2·43	10
..	2·29 vw	..	..	..	..	2· 8 w	2·28	2·28 mw	2·282	12	..	..	..	..
2·12 mw	2·12 m	2·14 m	..	..	..	2·12 w	2·12	2·12 mw	2·128	9	2·16 m	..	2·10	50
1·98 mw	1·99 w	1·98 w	2·09*	2·01*	..	2·04 w	1·99	2·04 mw	1·980	6	2·01 w	2·05*	..	..
1·82 m	1·82 m	1·81 m	..	1·83 w	..	1·82 m	1·82	1·82 ms	1·817	17	..	..	..	..
1·67 m	1·68 w	1·66 w	..	..	..	1·66 w	1·66	1·66 m	1·672	7	..	..	..	..
..	..	..	..	..	..	..	..	..	1·659	3	..	..	1·714	40
1·52 m	1·54 m	1·51 w	..	1·54 w	..	1·54 w	1·54	1·54 m	1·541	15	..	..	1·615	60
..	1·45 w	..	..	..	..	1·47 w	1·43	1·49 w	1·453	3	..	..	1·484	70
..	..	..	..	..	..	..	..	1·43 vw	1·382	7	..	..	..	..
1·37 m	1·37 m	1·38	..	1·38 w	..	1·38 m	1·38	1·38 m	1·375	11	..	..	..	..
..	..	..	..	..	..	..	..	..	1·372	9	..	..	1·326	10
..	..	..	..	..	..	..	1·29	1·29 vw	1·288	3	..	..	1·279	30
..	..	..	..	..	..	..	..	1·247 vw	1·256	4	..	..	..	..
..	..	..	..	..	..	..	1·185	1·185 w	1·184	4	..	..	..	..
..	..	..	..	..	..	..	..	1·177 w	1·180	4	..	..	..	..

* Diffuse rings. w : Weak. ms : Medium strong. vs : Very strong. vw : Very weak. m : Medium. s : Strong. vvw : Vrey-very weak. mw : Medium weak.

α-quartz are also given. It may be seen that the results obtained from the present study are in close agreement with the values for α-quartz. The fossil X-ray diffraction patterns (Figs. 12, 13, 14 and 15) can be compared with the pattern given by pure α-quartz powder (Fig. 11).

Discussion

Thus it appears that the silica in these diatoms, which are both freshwater and fossil diatoms, is α-quartz. The only anomaly is the result obtained from the study of untreated samples of *Isthmia nervosa* which presents a problem. Is there a difference between the silica as present in living diatoms and the silica in the treated diatoms which are dead, and the fossil diatoms? One solution, that suggests itself, is that there is some amorphous material which clouds the X-ray diffraction patterns and that this is removed either by chemical clearing using potassium dichromate and sulphuric acid, or during fossilization in various degrees. This naturally leads on to another question. Is the silica purely an inorganic deposition of α-quartz, or is there an organic substance in these frustules as well? If there is such an organic substance, what is its relationship with the silica which is α-quartz?

Liebisch (1929–30) does not believe that there is an admixture of organic material and that the silica is laid purely as an external layer. Mangin (1908), [*see* also Desikachary (1956)], feels that the silicate is deposited within the substance of a pectic material. Brieger (1924) also says that the silica is deposited in the shell as an organic complex. A large number of organic silicates are now known; but none have been identified so far from the diatoms. The results obtained from the present investigations agree so well with α-quartz, that the possibility of its being some other silicate seems out of question. However, an organic substance has been reported from fossil diatoms. Hahn (1925) has reported a gel-like protein (cornuit) in Kieselguhr from the deposits of Luneburg earth. It is albuminous and contains 2·8% dry substance and 0·07% ash, chiefly a diatomaceous residue. The diffusion of dyes into the gel, the adsorption of dyes and the swelling correspond to gelatin. The cornuit sol has a higher viscosity and surface tension than H_2O. The protective action of the sol was 30 times stronger than gelatin.

(*i*) *Origin of diffuse rings in untreated present-day diatoms.*—In view of this evidence, namely that a gelatin-like protein is probably present in diatoms, the X-ray diffraction pattern of thermally denatured collagen, which is practically the same as that of gelatin, was obtained. This is shown in Fig. 4. It will be noticed that the pattern is very similar to that of silica gel,

* Diffuse rings. w : Weak. ms : Medium strong. vs : Very strong. vw : Very weak. m : Medium. s : Strong. vvw : Very-very weak. mw : Medium weak.

and as will be seen from Table I, the broad maxima also correspond to the same spacings in both the cases. Thus, it is perfectly possible that there is a large amount of protein in the fresh untreated diatoms and that the X-ray pattern of the diatom (*e.g.*, Figs. 1 and 2) is essentially that of the protein. When the protein is removed by cleaning, the pattern of α-quartz shows up (Fig. 5).

(*ii*) *Occurrence of α-quartz in fresh diatoms.*—It may be mentioned that the X-ray patterns of most denatured proteins (*e.g.*, albumin, etc.) are alike and are very similar to Fig. 4. On the other hand, they are also similar to that of silica gel. However, silica gel is not readily dissolved by treatment with sulphuric acid and dichromate, nor is it converted to α-quartz by this treatment (*cf.* Figs. 3 and 3 *a*). Consequently, the α-quartz must be originally present in the diatom itself and it has been masked by the large amount of proteinous material which is present in the fresh diatoms. In the fossil diatoms on the other hand, most of the protein would have been removed, so that they give the pattern of α-quartz very clearly. It is significant to note that the rings of α-quartz given by the fossil diatoms are quite sharp and that they extend right up to the back reflection region (note in particular the rings at the extreme left and right in Figs. 13, 14 and 15). This shows that the material occurs in a well crystallised form.

(*iii*) *Probable occurrence of pectin.*—It will be readily noticed, on comparing the diffraction pattern of α-quartz (Fig. 11) with those of the fossil diatoms in Figs. 12–15, that there are a number of additional lines in the latter, particularly within the strongest line of spacing $d=3{\cdot}34$ Å of α-quartz. A study of these indicated that these were close to those of pectin (*see* Table I). Consequently, the diffraction pattern of a mixture of α-quartz and pectin in equal proportions was obtained and is shown in Fig. 16. The intensity distribution as well as the spacings of the diffraction rings in this pattern are seen to be in good agreement with those observed in some of the fossil patterns, particularly the well-crystallised fossil diatoms from Lake Sumner in New Zealand (Fig. 15). Thus, there seems to be evidence to show that pectin is present in the diatom frustules. The near identity of the pectin and quartz spacings seems to indicate that oriented crystallization of pectin with silica is present in the diatom.

(*iv*) *Occurrence of other components.*—In *Isthmia nervosa* diffraction rings which are diffuse and which probably belong to an organic substance were observed with a spacing of 2·1 Å. Silica gel does give such a ring faintly at 2·05 Å. On the other hand, gelatin and degraded collagen also give such a ring. Consequently, if silica gel is eliminated on the grounds that

it cannot be removed by washing with acid, there seem to be good grounds for assuming that protein (probably related to gelatin) is present as a component of the frustule. There are a few other rings which are weak in intensity and are not as yet correlated with α-quartz. The possibility that these rings may not be due to pectin, but may belong to some iron or aluminium compound was also investigated. It is possible that some of these additional rings observed may belong to Fe_3O_4. The spacings for Fe_3O_4 are also given in Table I. But they do not rule out the presence of pectin, since there are still additional lines unaccounted for by Fe_3O_4. However, no aluminium oxide or any of its modifications could be detected from the diffraction patterns.

It is probable that the proportion of the organic substance varies with the species. By the partial removal of these organic substances by alkali or acid treatment (*see* Jorgensen, 1955) the silica is rendered proportionately soluble. One does not know whether these organic substances play a role in making the frustule insoluble ordinarily. There is need for study of this problem in greater detail.

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Summary

This paper describes the X-ray diffraction studies carried out on a large number of present-day, as well as fossil diatom frustules. From the diffraction patterns given by the various specimens, it has been concluded that the silica present in diatom frustules is not in an amorphous or sub-colloidal state as was supposed by previous workers but that it is crystalline α-quartz. Although crystalline α-quartz is present in present-day diatoms, the degree of crystallisation is much less than in the fossilized specimens. In addition to the crystalline quartz content, there is present in all diatoms an organic component which might possibly be a protein. In the present-day diatoms this organic component occurs in considerable proportion so that its X-ray diffraction pattern tends to mask the pattern due to crystalline α-quartz. On fossilization, however, a considerable amount of the protein content is lost, while the silica content becomes more predominant, and more and more crystalline with time. Evidence for the occurrence of pectin in diatoms is also presented.

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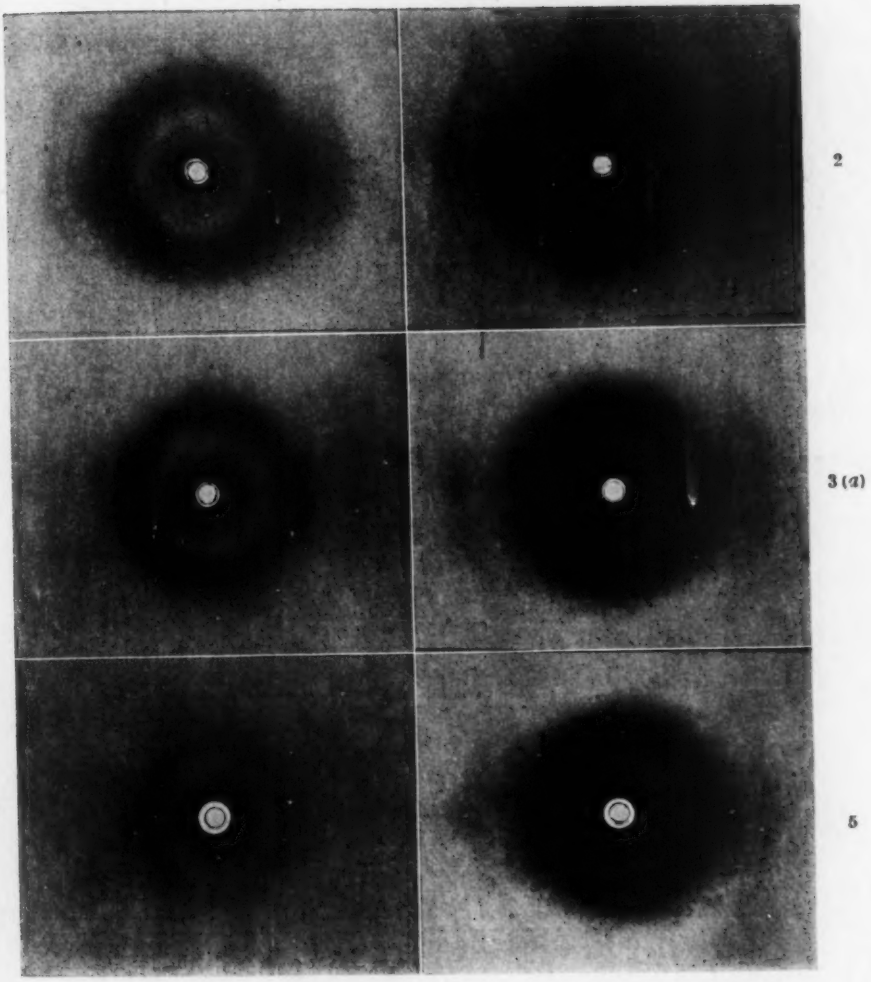

FIGS. 1–5

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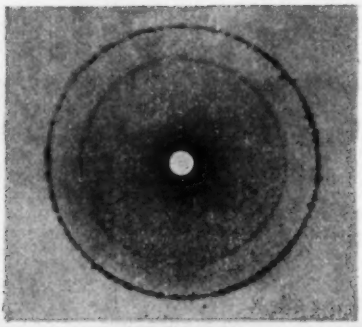

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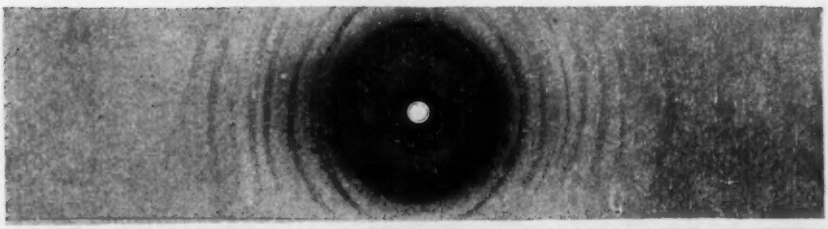

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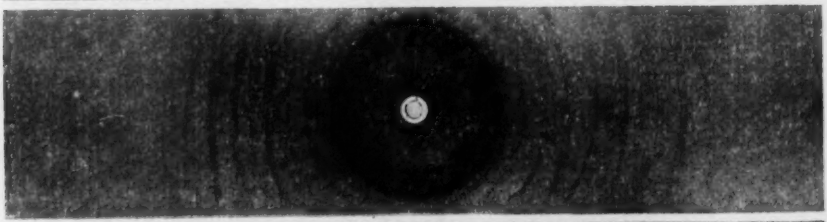

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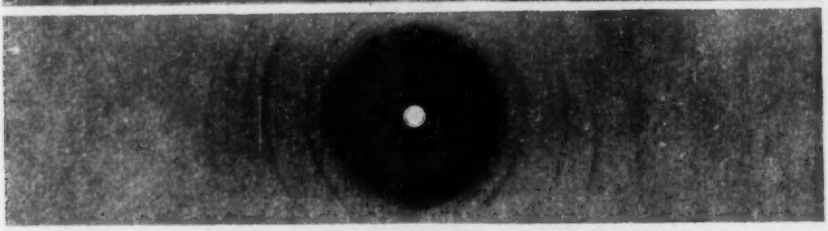

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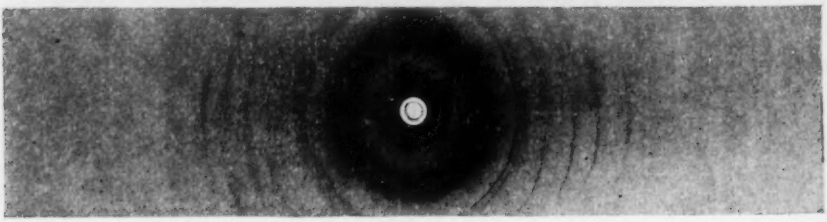

FIGS. 6–10

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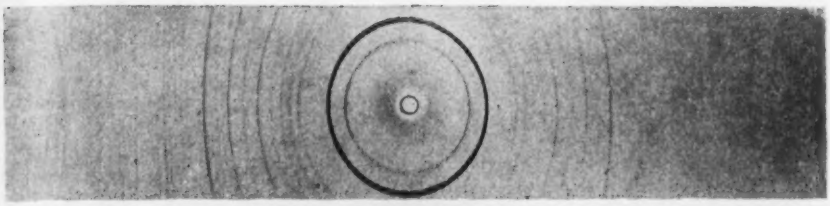

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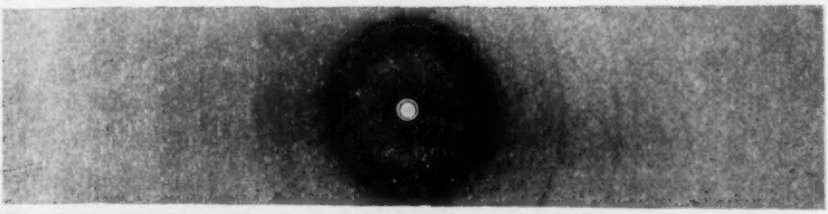

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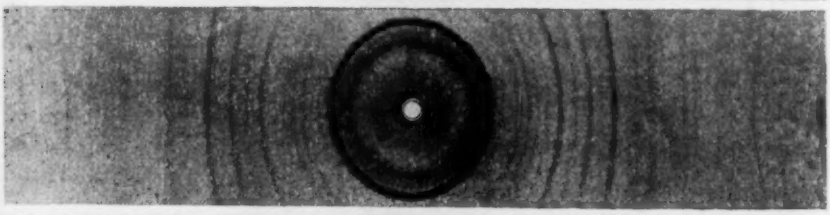

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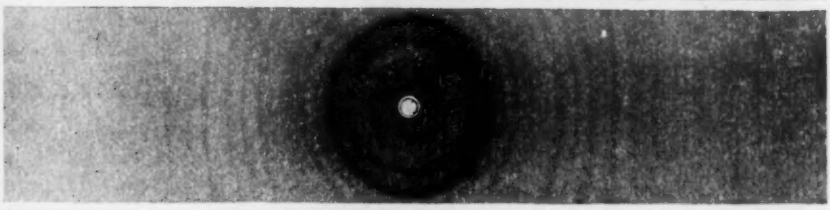

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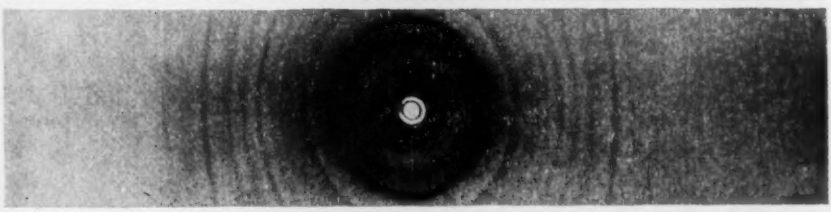

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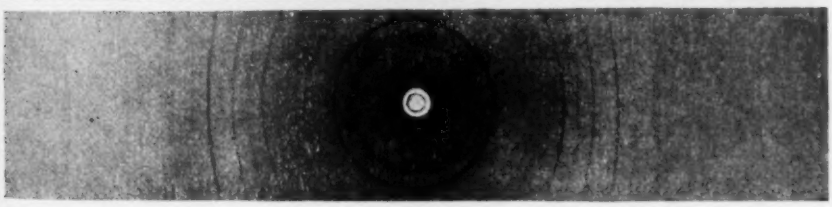

FIGS. 11–16

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Explanation of Plates

[All figures are X-ray diffraction powder patterns obtained using Ni-filtered CuKα radiation and a cylindrical camera with R = 3 cm. (unless otherwise specified).]

Plate IX

Figs. 1–5. Fig. 1. X-ray pattern of diatoms of *Isthmia nervosa* dried in air. Fig. 2. X-ray pattern of diatoms of *Isthmia nervosa* preserved in rectified spirit. Fig. 3. X-ray pattern of untreated silica gel powder. Fig. 3 (*a*). X-ray pattern of silica gel powder treated with sulphuric acid and potassium dichromate. Fig. 4. X-ray pattern of thermally denatured collagen. Fig. 5. X-ray pattern of *Isthmia nervosa* after treatment with sulphuric acid and pottassium dichromate.

Plate X

Figs. 6–10. Fig. 6. X-ray pattern of specimens as in Fig. 5, taken on a flat film in a microcamera, and enlarged to correspond to a distance D = 4 cm. Figs. 7, 8 and 9. X-ray patterns of mixtures of *Cyclotella meneghiniana* and *Gomphonema parvulum* diatoms in different proportions. Fig. 10. X-ray pattern of diatoms of *Fragilaria brevistriata*.

Plate XI

Figs. 11–16. X-ray pattern of powdered crystalline α-quartz. Fig. 12. X-ray pattern of fossil diatoms from Florida, U.S.A. Fig. 13. X-ray pattern of fossil diatoms from Lampoc, U.S.A. Fig. 14. X-ray pattern of fossil diatoms from Oomaru, New Zealand. Fig. 15. X-ray pattern of fossil diatoms from Lake Sumner, New Zealand. Fig. 16. X-ray pattern of a mixture of α-quartz and Pectin in equal proportions.

THE QUADRANT PROEMBRYO OF *EPITHEMA CARNOSUM*

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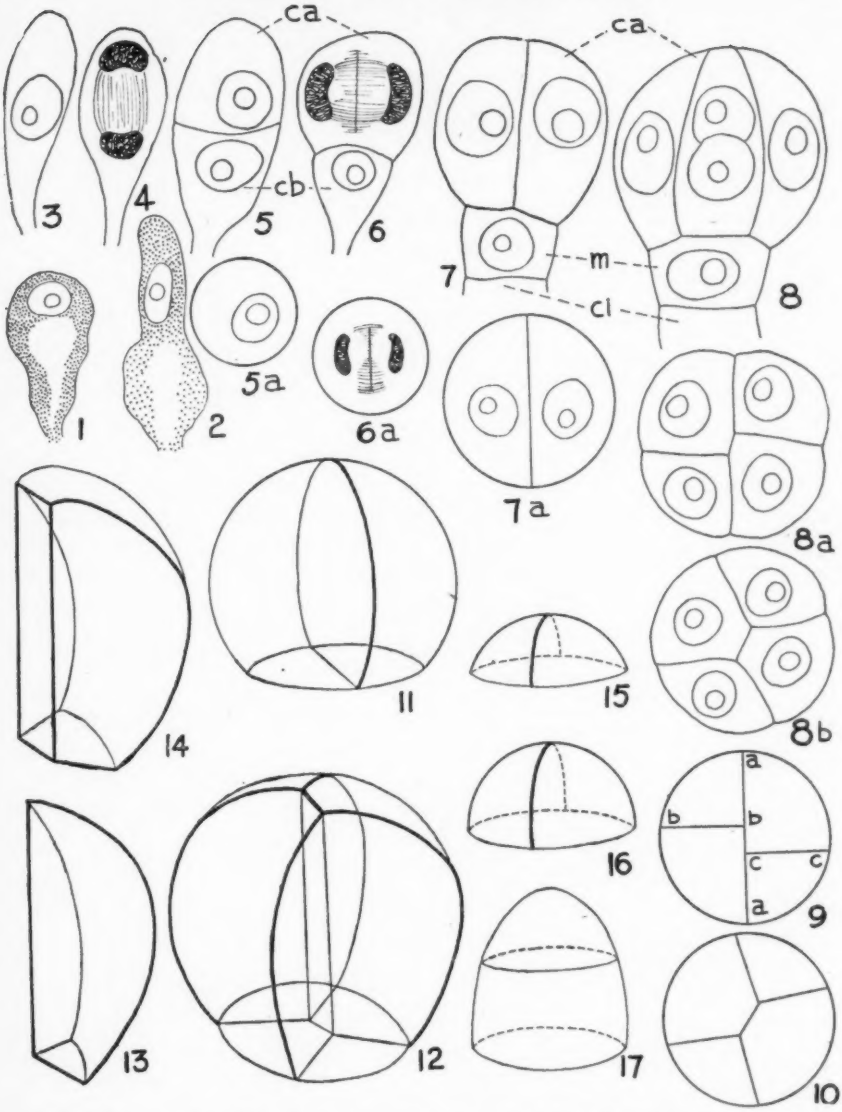
The physical basis underlying the patterns of soap bubbles in froth attracted the attention of biologists, mathematicians and physicists. Biologists were interested in the problem purely in the hope that a study of the soap bubble might throw light on the form of animal and plant cells. A brilliant and comprehensive review of the historic papers on the subject has already been presented by Thompson (1952), in which he has dealt with the form and growth of plant cells as well. Of particular interest is his analysis of the size and form of proembryonal cells in relation to the phenomenon of surface tension. However, all these inquiries have emphasized the mathematics and physics of the soap bubbles. The object of the present study is to analyse the role of certain physical and biochemical factors possibly operating during the early segmentation of the zygote in *Epithema carnosum*. Stages leading up to the formation of the quadrants have been discussed in the present contribution and a consideration of octant-formation will be taken up separately.

The sequence of early divisions in the zygote.—The first division of the zygote (Figs. 3, 4) is followed by the laying down of a transverse wall (Fig. 5). The basal cell *cb* divides transversely to form *m* and *ci* (Figs. 6, 7). The terminal cell *ca* divides by a vertical wall. Each of the daughter cells now divides by means of a vertical wall which is oriented at right angles to the common wall (Figs. 8, 8 *a*, 9). Thus the quadrant stage is attained.

Transverse sections through the terminal cell at successive stages of development of quadrants indicates that the first vertical division results in two almost hemispherical cells (Figs. 6, 6 *a*, 7, 7 *a*). In other words, the wall cuts the spherical terminal cell *ca* along its vertical diameter (Fig. 11). Although the second vertical division in the two daughter cells takes place at right angles to the first, the walls are not laid down along the radii; instead each of them cuts the first vertical wall at a point short of the geometric centre of the sphere (Figs. 8 *a*, 9). Thus, the division of the daughter cells of *ca*



FIGS. 1–17. Fig. 1. The unfertilized egg. Fig. 2. The initiation on the zygotic tube. Fig. 3. Tip of the zygotic tube prior to division. Figs. 4 and 5. First division of the zygote. Figs. 5 *a* and 6 *a*. Transections through *ca*. Figs. 6 and 7. First division of terminal cell *ca* and that of the basal cell *cb*. Figs. 7 *a*, 8 *a* and 8 *b*. Transections through the terminal tier during successive stages of quadrant development. Fig. 8. Quadrant proembryo. Figs. 9 and 10. Same as in 8 *a* and 8 *b*; diagrammatic. Fig. 11. Reconstructed three-dimensional view of *ca*. after first partitioning. Fig. 12. Reconstructed three-dimensional view of quadrant cells *in situ*. Figs. 13 and 14. Reconstructed three-dimensional view of quadrant cells shown separately. Figs. 15–17. Adopted from Thompsom (1952). For explanation see text.
Magnifications: Figs. 1–8, 5 *a*, 6 *a*, 7 *a*, 8 *a*, 8 *b*. all × 600.

are independant and the walls laid down during cytokinesis do not intersect the first wall at one and the same point.

In Fig. 9, *aa* represents the first vertical wall in the terminal cell while *bb* and *cc* connote the second set of vertical walls in the daughter cells. As stated earlier, the second set of walls form a right angle with the first vertical wall. The span between *b* and *c* along *aa* is what has been designated as the *polar furrow* (Thompson, 1952). As a consequence of such a pattern of growth of the four resulting cells the opposite ones possess similar features. This is easily understandable in view of the unequal size of the grand-daughter cells of *ca* (Figs. 8 *a*, 9).

Hand in hand with the divisions in the terminal cell *ca*, changes in shape of the constituent cells take place. One of the important results of this combined phenomenon is the conventional definition of the *polar furrow* (Fig. 10). Now two opposite cells of the four-celled group appear more or less triangular while the other two trapezial in transectional views (Figs. 8 *b*, 10). This stage in ontogeny marks the advent of bilateral symmetry in the proembryo (*see* also Thompson, 1952, p. 489). The three-dimensional shape of the triangular and trapezial cells are represented in Figs. 13 and 14 respectively while in Fig. 10 the topographical relationship of the concerned cells in the quadrant proembryo is shown.

Factors operating during the early divisions of the zygote.—The phenomenon of surface tension has been recognised as the important physical factor bringing about the characteristic patterns of " cell-walls " in a froth of soap bubbles. It is well known that when a fluid is in contact with a solid the surface energy of the system is proportional to the area of contact. The system tends towards equilibrium or a condition of minimum potential energy by the greatest possible reduction of the surface in contact. In other words, the effect of surface tension will be manifested in surfaces of minimal area. This principle has already been shown to operate on the grouping of cells and nature of cell partitions (Thompson, 1952).

Hofmeister (1863) maintained that cell partitions are formed at right angles to the principal direction of growth (*i.e.*, the long axis). Sachs (1877) declared that in all tissues cell-walls cut one another (at the time of formation) at right angles. Reinke (1880) questioned the validity of this explanation. He maintained that the rectangular symmetry was a secondary result of growth. This view was shared by a number of botanical writers.

Thompson (1952) points out that Sachs' rule is limited to those cases where one cell-wall grows stiff and another impinges upon it. Berthold

(1886) adopted the principle of minimal areas and compared the arrangement of cell partitions with those assumed by a system of weightless films under the influence of surface tension. Simultaneously Errera (1886) definitely laid down that cell partitions obey the laws which operate on the soap bubbles in contact. Errera's law runs as follows: " A cell-wall, at the time of its formation, tends to assume the form which would be assumed under the same conditions by a liquid film destitute of weight. " According to the corollaries of this law only three films meet at one edge and at co-equal angles.

Wardlaw (1955) has enumerated the probable biochemical factors operating during the early divisions of the zygote. The unfertilized egg is considered to possess a definite physical and biochemical organization. In the case of *Epithema carnosum* it has a characteristic conical form with a rounded chalazal end (Fig. 1). The cytoplasm is denser at the rounded end of the cell where the nucleus is situated; a conspicuous vacuole is located in the tapering micropylar part. It is likely that the vacuolated end differs from the nucleated end in the concentration of metabolites with the result that a gradient is established. In fact, the polarity of the egg cell is evident even prior to fertilization. The long axis which connects the apical and basal poles could be demonstrated as soon as the egg-apparatus becomes organised. Hence the egg cell itself can be considered as possessing a highly complex biochemical and physical organization. The membrane of the egg cell being a tenuous structure is comparable to *weightless films* acted upon by surface tension as well as by internal forces.

Fertilization is an important event in so far as it affects the genetic constitution of the egg which as a consequence becomes transformed into the initial cell of the sporophytic generation. The visible differentiation of cytoplasm of the zygote remains relatively unaltered even after fertilization. It is of interest to note that the rate of growth of the zygote is not equal in all directions. That part of its wall adjoining the nucleus (apical pole) grows into a tubular structure (Fig. 2). The nucleus migrates into the tube and always tends to occupy the extreme tip. The growth in length of the zygotic tube ceases as soon as it reaches the middle part of the embryo-sac. Further growth of the tube is concerned not with the process of elongation but with an increase in diameter, as a result of which a club-shaped form is attained. This change in the mode of growth is obviously an expression of the gene-controlled metabolic system. It may be remarked that the cytoplasmic condition in that part of the egg cell which is left behind near the micropyle indicates degeneration.

The early growth of the zygote obviously resuts in an increase in surface area. This leads to a condition when equilibrium between the surface

forces and internal forces has to be maintained through the ensuing cell division. However, cell division follows nuclear division. The place of the partition wall depends on the shape of the nucleated tip of the zygotic tube. On the basis of physical forces of the type of surface tension, the wall formed after karyokinesis should be a partition of minimal area, that is, in the transverse plane. Speaking of the *areæ minimæ*, Thompson (1952, p. 574) writes, " .... if we have a spheroidal body less than a hemisphere.... it is obvious that the smallest partition by which we can divide it into two halves is a median vertical one " (Fig. 15). In the case of a hemisphere, the vertical wall is again the partition of minimal area (Fig. 16). Upon distorting the hemisphere so as to result in a more elevated conical body or in a cylinder with a spherical cap, a transverse partition constitutes the minimal area (Fig. 17). The tip of the zygotic tube which is on the verge of division corresponds exactly to the last-mentioned type and hence we can explain the disposition of the first wall in the zygote on a physical basis. However, attention should be drawn to the factors involved in the first nuclear division. Internal metabolic factors may be active in this respect. We have to consider what factors operate on the orientation of the metaphase spindle which is the basis of deposition of a transverse wall. It is likely that the very physical factors operating on the surface also influence the alignment of the spindle, and hence of the orientation of the wall. However, the play of gene-controlled metabolic factors during this phase of zygotic growth cannot be overlooked, as a gradient system in the histology of the zygote has become established even before and after syngamy. Until more information becomes available about the internal (egg and zygote) and external (embryo-sac) gradient systems, it will not be possible to clearly state the relative proportions and magnitude of the physical and biochemical factors that operate during the first segmentation of the zygote.

It may be pointed out that the terminal cell *ca* soon after its formation, assumes a hemispherical form and a median vertical wall in this cell represents the partition of minimal area. Even though it might appear that the forces of surface tension play a major part in the orientation of the phragmoplast as well as of the ensuing partition wall, the gene-controlled mechanism which brings about a specific form of the zygote prior to its division, is more fundamental. It may be added in parenthesis, that the two-celled embryos whose terminal cell is partitioned transversely—the Solanad, Chenopodiad and Caryophyllad types of Johansen (1950)—may be explained on the basis of the foregoing arguments. After the first division of the zygote, in these instances, the terminal cell assumes a cylindrical form with a rounded end. The wall of minimal area by which such a cell divides is a transverse one.

The assumption of the specific form which is subject to analysis on physical basis is an expression of the gene-controlled biochemical factors.

The two hemispherical cells of the terminal tier of the proembryo soon undergo a division in a vertical plane at right angles to the previous partition. However, it must be emphasized that the newly formed partitions in the two cells do not interesect the first-formed wall at the same point, but leave a small length of it to form an intermediate gamut, whose upper edge is the *polar furrow*. This newly defined structure can be distinctly demonstrated in surface views of the spherical mass of four cells at succeeding stages. In such an unstable configuration (Fig. 9) only three partitions meet at any given edge. After stable equilibrium is attained the concerned walls are oriented at co-equal angles (Fig. 10).

If we consider the interaction between two adjacently placed cells in division it is apparent that even though they are acted upon by similar surface forces the internal forces tend to affect the position of the spindles as well as of the ensuing partition walls. On the basis of the postulates of Gerassimova (1957) repulsion between the two dividing nuclei could be the cause to explain why the resulting walls do not cut the first vertical partition at the same point. Thus it appears that the length of the *polar furrow* would depend on the magnitudes of the internal forces acting upon the dividing nuclei.

On the basis of the dynamics of growth, the quadrant stage may be considered as representing a phase of insignificant increase in surface area but of active cell division. The quadrant cells become subjected to localised growth in specific directions. This probably explains why a state of perfect stable equilibrium is not reached in the embryonic system at any ontogenetic level. It is less probable that there are static periods in the ontogeny of an embryo. It is more likely that growth phases succeed one another in the form of waves with transitory intervals of seeming stabilization.

Even though the patterns of cell aggregates could be explained on the basis of physical forces, the gene-controlled metabolic system also appears to play an important role. Therefore, although similar patterns of divisions may ensue during the early development of the embryos in diverse groups of plants, the gene-controlled metabolic systems underlying these patterns may not all be alike. This is borne out by later patterns of ontogeny leading to the characteristic exomorphic and endomorphic features distinctive of the taxa. The genes concerned in the process of late ontogenetic diversification may not be active during early stages. Summing up, it may be postulated that the characteristic form of cells and cell aggregates at any level of development are the results of, and vary according to the magnitudes of

internal forces of the gene-controlled metabolic systems and that of the external forces like surface tension.

SUMMARY

The zygote of *Epithema carnosum* divides by a transverse wall. The terminal cell undergoes division by a vertical wall. The next division in the daughter cells occurs in the same plane but at right angles to the first-formed partition. During this division the partition walls meet the original vertical wall at right angles. After the completion of the two divisions, cell readjustments tend towards a state of minimal potential energy. The quadrant cells at this stage come to possess walls disposed as in a group of four soap bubbles in contact and in a state of stable equilibrium. The possible conjoint operation of physical and biochemical forces during the early divisions of the zygote is discussed.

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USE OF AUREOMYCIN IN FISH PRESERVATION AND EFFECT OF HEAT ON THE ANTIBIOTIC-TREATED FISH

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Introduction

The use of certain chemicals like sodium nitrite in very small quantities incorporated in ice or chilled sea-water in the preservation of fish was found to be effective in the control of spoilage of fish. As a further step forward in the preservation of flesh foods, Tarr and his associates (1944, 1948 *a*, 1948 *b*, 1950) were the pioneers to demonstrate that the antibiotics of the "wide spectrum" group, Chlorotetracycline (CTC) and Oxytetracycline (OTC), could be used with very great advantage to retard the spoilage of fresh, chilled and iced fish. Much interest has been shown in the use of antibiotics as preservatives for food by scientists throughout the world. This interest has been aroused by the relatively dramatic effects of exceedingly small concentrations of certain of these compounds in retarding the bacterial phase of spoilage of fish. CTC has been found to be more efficaceous than OTC. CTC has been incorporated in ice used for icing fish or in chilled sea-water in which they have been transported. Fresh fish has also been subjected to a dip in a solution containing the antibiotic for short periods before it is stored in cold stores or iced. The keeping quality of the antibiotic-treated fish has been reported to be considerably enhanced and the consumption of such a fish is also reported to be harmless as these antibiotics are heat-labile. In our country Velankar and Kamasastri (1958) reported that CTC at 5 p.p.m. level in ice used for icing fish had a favourable effect in the keeping quality of fish, while Visweswariah *et al.* (1959) found that mere dipping of the fish in a CTC solution and storing at 30° C. did not improve the keeping quality whereas protracted immersion of fish fillets in dip solutions and subsequent storage at 30° C. enhanced the keeping quality two-fold. Visweswariah *et al.* (1960) had also reported their findings on the effect of CTC on freshwater fish fillets and are of opinion that

CTC in combination with 5% NaCl had no beneficial effect as compared to aureomycin dips alone.

The purpose of this paper is to present the results achieved in the uptake of CTC by fish fillets by dipping and the effect of normal washing and heat on such preserved fish muscle during culinary preparations.

MATERIALS AND METHODS

Fresh fillets devoid of skin were prepared from locally available seer fish in its prime quality and were immersed at room temperature in a tap-water solution containing 20 p.p.m. of the antibiotic, aureomycin, exactly for 1 minute, and were allowed to drain for 10 minutes after which they were wrapped in wax paper and kept in cold storage at 0 to 3° C. for subsequent observations and analysis.

The assays of the antibiotic in the flesh samples were done by the pad plate method as outlined by Grady and Williams (1953) on the acid acetone extracts of fish muscle.

For studies on the heat treatment of the CTC treated fillets, samples were cut from the fillets, to which, water, equal to three times its weight, was added and the contents immersed in a water-bath maintained at different temperatures. The effect of leaching the fillets with running water at room temperature from 5 minutes to 30 minutes was also studied. The fillets were subjected to deep fat frying and grilling procedures in a commercial restaurant and the CTC assayed on such fillets. The results are given below.

Table I gives the results of the assay of CTC picked up by the fish fillet in the different layers after the initial dipping in a 20 p.p.m. CTC solution for 1 minute.

Immediately after dipping the fish fillet in the dip solution, the CTC was found mostly on the surface layer of a fillet. As time goes on, there is a certain amount of CTC getting into the flesh but the rate of penetration is slow excepting in the tail portion where a measurable quantity of the antibiotic was found. This is to be explained as due to the texture of the flesh in this particular portion of the fillet where a large number of "crevices" or "channels" of muscle layers are found and these may probably facilitate the antibiotic solution to find its way deeper. Ultra-violet ray examination of the whole fillet also supports the figures in Table I. The characteristic fluorescence due to the antibiotic under the ultra-violet rays showed that the inner core of the thick portion of the fillet (Nape and central

TABLE I

Quantity of CTC in p.p.m. picked up by fish fillets during dipping in a 20 p.p.m. solution

Portion of the fillet		Days after storage at 3° C. (CTC in p.p.m.)				
		0	1	2	4	8
NAPE	Top layer ..	1·4	0·90	0·8	0·8	0·92
	Middle layer ..	Nil	Nil	0·01	Nil	Nil
	Bottom layer ..	1·02	0·50	0·3	0·32	0·80
CENTRAL	Top layer ..	0·88	1·2	0·8	0·96	0·08
	Middle layer ..	Nil	Nil	Nil	?	Nil
	Bottom layer ..	0·96	0·62	0·7	0·81	1·08
TAIL	Top layer ..	0·79	0·84	0·61	1·26	1·32
	Middle layer ..	0·02	0·02	0·25	0·18	0·02
	Bottom layer ..	0·31	0·30	0·4	0·2	0·60

portions) was devoid of any CTC which is in conformity with the observations of Tomiyama *et al.* (1957) with bonito fillets whereas a certain quantity of CTC was present even in the inner core in the case of the tail portion.

The amount of CTC on the surface of a fillet is not always uniform in the same fillet nor in the different fillets examined after cold storage. It was also noted under the ultra-violet rays that the brownish muscle probably due to its fatty nature, occurring in patches in a fillet do not pick up the antibiotic so readily or uniformly as the white muscle. This is especially striking in the tail portion of the fillet where the skin side (underside) of the muscle is not really white but brownish.

The above results obtained by a physical examination of a fillet under ultra-violet rays were confirmed by actual assay of the CTC in the different layers from the central portion of a fillet. The results are given in Table II.

It could be seen from Table II that the amount of CTC picked up by the fillet is neither uniform in the different fillets nor the CTC was

TABLE II

Quantity of CTC in p.p.m. in the different layers of muscle sections cut out, from the thickest part (central portion) of a fillet

Section No.	No. of days of storage of the fillet at 3° C.			
	1	2	5	7
1	1·02	0·92	0·82	0·92
2	0·01	Nil	0·2	0·2
3	Nil	Nil	?	?
4	Nil	Nil	Nil	Nil
5	Nil	0·01	Nil	?
6	0·1	0·13	0·2	0·25
7	0·79	0·75	0·84	1·32

(Each of the 7 sections was between 3 to 4 mm. in thickness)

found in the innermost core of the muscle. Even storage of the fillet at 3° C. over 7 days has not enabled the antibiotic to diffuse through the inner sections. This may have a pratical significance in all problems on the handling of fresh fish. The innermost core of a fish muscle is comparatively free from bacteria and unless the fish is handled properly and effectively soon after the catch, bacteria will penetrate into the interior, both from the skin side as well as from the gut cavity side. In the practical application of aureomycin dips for fish fillets to prolong its shelf life in cold storage if the dip is to be effective, immediate action must be taken to keep the surface bacteria under check. The dipping of a fish fillet of second quality will not in any way enhance the shelf life of the cold-stored product as the aureomycin does not penetrate deep into the muscle and retrieve the damage that has already been done by the bacteria in the interior parts of the muscle.

Effect of leaching action of water on the fillets at room temperature.— Prior to actual usage of the fish fillet for cooking, the fillets are usually washed and then prepared for the table. Experiments were conducted to find out as to what extent the leaching action of water removes the antibiotic from the fish muscle when fish fillets were left in a gentle stream

of flowing water in the laboratory for varying periods of time and the CTC assayed. The results are given in Table III.

TABLE III

CTC in p.p.m. in fish fillets which were immersed in flowing water

	Time of immersion of fillet			
	5 mts.	10 mts.	15 mts.	30 mts.
Amount of CTC present in the fillet prior to leaching	0·66	1·06	0·94	1·4
Amount of CTC present in the fillet after leaching with water	0·30	0·40	0·38	0·62
Per cent. of removal of CTC from the fillet by the flowing water	54·5	62·2	59·5	55·7

The results shown in Table III indicate that the CTC is leached out from the fillet by the water at room temperature to the extent of 54 to 62%, but the quantity so removed does not seem to vary very much with increasing time.

EFFECT OF HEAT

It has been proved by Tarr *et al.* (1954), Tomiyama *et al.* (1957) and Bohonos *et al.* (1954) that CTC in foods is stable at low temperature but gets readily destroyed or inactivated on heating. The results of experiments conducted at the Torrey Research Station (1956) show that less than 0·1 p.p.m. CTC can still be detected in antibiotic-treated fish which was steamed for 30 minutes but this quantity was considered to be negligible for a health hazard. Even though heat inactivates CTC bacteriostatically, natural colloids and other substances present in flesh foods seem to retard this change and consequently some consideration has been given to the problem of CTC residue in cooked flesh foods. Experiments were conducted at this station on fish fillets dipped in a 20 p.p.m. CTC solution and the effect of normal heating procedures on the fillet was investigated. Table IV shows the results of keeping the fish fillet completely immersed in water at varying temperatures for different periods of time.

TABLE IV

Effect of heat on CTC-treated fish fillets

Experiment No.	Quantity of CTC present originally (p.p.m.)	CTC present after heat treatment in p.p.m.										
		Temp. 70° C.				Temp. 80° C.				Temp. 98° C.		
		Time in minutes										
		5	10	15	30	5	10	15	30	5	10	15
1	0·66	0·058	Trace	Nil	Nil	Nil	Nil	Nil	Nil	Nil	Nil	Nil
2	0·96	0·13	Nil	Nil	Nil	Nil	Nil	Nil	Nil	Nil	Nil	Nil
3	1·04	0·056	Nil	Nil	Nil	Nil	Nil	Nil	Nil	Nil	Nil	Nil

The CTC is completely destroyed in fish fillets when kept at 70° C. for 10 minutes and at higher temperatures within periods shorter than this. However at 70° C. the CTC is not completely destroyed when the fish fillets are immersed for 5 minutes (86 to 94% only of the original CTC having been removed) while immersion at this temperature for longer periods is effective.

The effect of heat under conditions obtainable in the trade was next investigated. Fillets dipped in the CTC solution and stored in cold storage were distributed to a commercial restaurant and subjected to grilling and deep fat frying processes in the normal way. The results of assay of CTC in the samples prepared in the above manner are given in Table V. It may be seen from Table V that the C.T.C. is not destroyed completely under conditions normally obtainable in trade for grilling and frying while cooking in water destroys completely the antibiotic present. Grilling can inactivate 78 to 100% of the original CTC and deep fat-frying 85 to 100%. This is contrary to the findings of Pasternack *et al.* (1956) who state that the antibiotic is destroyed by heat as could be encountered in cooking, *viz.*, boiling, broiling, baking and frying. No measurable residual antibiotic was found in their case after 10 to 12 minutes of heat. Kohler *et al.* (1955) are also of the same opinion working with poultry foods. In the experiments given above, the residual CTC even in the fried and grilled samples are less than 0·12 p.p.m. only, which limit, under the available evidence, cannot be a great objection in the use of antibiotics for preservation of fish nor can it be considered a health hazard.

TABLE V

CTC assay in fillets which were subjected to grilling and deep fat frying

Sample No.	CTC present before heat treatment (p.p.m.)	Amount of CTC present after grilling (p.p.m.)	Per cent. destroyed	Amount of CTC present after deep fat frying (p.p.m.)	Per cent. destroyed
1	0·92	Nil	100	0·12	87
2	0·92	0·12	87	Traces	97
3	1·04	0·06	94	Nil	100
4	1·04	Nil	100	Nil	100
5	0·9	Nil	100	·12	87
6	0·7	0·076	89·1	·008	98·8

CONCLUSIONS

Fish fillet when dipped in CTC solution at 20 p.p.m. picks up the antibiotic only on the surface or just below it. It is not found in the innermost core of the muscle. The absorption of the CTC even on the surface is not quite uniform throughout a fillet. White muscle of a fish picks up the antibiotic more readily than the fatty layers or the brown-coloured portions of the muscle.

Washing the fillet with water prior to its preparation for the table removes a considerable portion of the antibiotic, the amount so removed ranging from 54 to 62% of the original amount.

Heating the antibiotic-treated fish with water at 70° C. and above for periods of more than 10 minutes or keeping the fish at 98° C. even for a short while completely inactivates or destroys the antibiotic. Frying and grilling the fish destroys the antibiotic to the extent of 87 to 100% of the original quantity present. The maximum quantity found in the latter cases was only 0·12 p.p.m. which can be considered to be innocuous.

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AZOTOBACTER SPP. IN THE RHIZOSPHERE OF SOME AGRICULTURAL CROPS

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The occurrence of *Azotobacter* Spp. in the rhizosphere of agricultural crops presents an interesting study especially in view of the reported success of inoculation of soft wheat with the organism[17] and the rhizosphere effects on soil microflora as observed by Lochhead and associates.[2, 8–11, 14]

Krassilnikov[6] found, however, that *Azotobacter* was unable to grow in the rhizosphere of wheat and was severely repressed in that of maize. Fedorov *et al.*[3] observed that *Azotobacter* Spp. present in the rhizosphere of perennial herbage, clover and timothy had low nitrogen fixing capacities. Excretions from roots of peas were soon found out to be more favourable for *Azotobacter* than those of maize. Tchan *et al.*[16] observed that heavy soils under certain grasses contained low numbers of *Azotobacter*. Irushkin[4] reported that certain actinomycetes in the rhizosphere of lucerne inhibited the growth and decreased the nitrogen fixing capacity of *Azotobacter*. Kudrina[7] noted that *Azotobacter* in the rhizosphere of certain wheats and lucerne were more active than those in the non-rhizosphere soil. Roy *et al.*[13] found that the *Azotobacter* occurred in the rhizosphere of jute in numbers 2–3 times that in the non-rhizosphere soil without any benefit to the crop.

During the present investigation, the effect of the rhizosphere of two cereals and two legumes on the distribution and nitrogen fixing capacity of the organism was studied. This was done by estimating the numbers of *Azotobacter* in the rhizosphere and in the non-rhizosphere soils of wheat, maize, berseem and *guar* showing good growth and also when the growth was stunted but with no apparent disease.

Experimental

Soil samples were collected aseptically from three unmanured fields each of wheat, berseem, maize and *guar* (cluster bean) from the rhizospheres under good and bad stand of the crops at the pre-flowering stage and from bare soils on the same fields from similar depths. Platings in silica plates,[14] treated with 2 c.c. of Jensen's agar, were made soon after.

The organism was isolated from 3–4 colonies of largest frequency in each plate and transferred to mannite agar slopes.[1] The characteristics of the genus were confirmed before determining their nitrogen fixing capacities in Jensen's medium[5] incubated at 32° C. for two weeks.

Results and Discussion

The numbers of *Azotobacter* Spp. in the rhizosphere and bare soils under different crops and their nitrogen fixing capacities are given in Table I.

Table I

Counts of Azotobacter *Spp. in rhizosphere and non-rhizosphere soils of different fields and their nitrogen fixing capacity*

Crop	Rhizosphere		Non-rhizosphere	Significance of differences
	Good growth	Stunted growth		
	Number of *Azotobacter* cells (hundreds/gm. of soil)			
Wheat ..	16·9±2·3	18·3±4·9	14·6±2·6	Not significant; $SE_m = \pm 2{\cdot}85$
Berseem ..	15·7±4·7	27·4±5·0	20·0±7·9	Not significant; $SE_m = \pm 8{\cdot}90$
Maize ..	33·6±2·0	18·6±1·0	20·1±1·0	Not significant; $SE_m = \pm 3{\cdot}11$
Guar ..	22·8±3·7	19·0±2·8	17·8±1·0	Not significant; $SE_m = \pm 1{\cdot}57$
	Nitrogen fixing capacity of *Azotobacter* Spp. (mg./gm. of sucrose Jensen)			
Wheat ..	11·2±0·3	10·7±0·6	12·0±0·0	Not significant; $SE_m = \pm 1{\cdot}14$
Berseem ..	10·2±0·8	9·7±0·3	9·0±0·1	Significant at 1%; C.D. $= \pm 0{\cdot}85$
Maize ..	15·5±0·6	13·9±0·5	13·9±0·7	Significant at 1%; C.D. $= \pm 1{\cdot}14$
Guar ..	14·0±0·8	13·5±0·3	13·5±0·1	Significant at 1%; C.D. $= \pm 0{\cdot}56$

The organic carbon, organic nitrogen and pH values of the rhizosphere and non-rhizosphere soils from different fields are given in Table II.

It could be seen from the data in Table I that there were no differences in *Azotobacter* numbers in the rhizosphere and non-rhizosphere soils in the wheat and *guar* fields, but there were significant differences in the same in the berseem and maize fields. In the case of the latter, rhizosphere of the

TABLE II

Organic carbon, organic nitrogen and pH values of rhizosphere and non-rhizosphere soils of different fields

Crop	Rhizosphere		Non-rhizosphere	Significance of differences
	Good growth	Stunted growth		
	Organic carbon (gm. % on moisture-free basis)			
Wheat	·43± ·05	·34± ·04	·45± ·04	Not significant; $SE_m = \pm 0{\cdot}0029$
Berseem	·47± ·03	·45± ·02	·47± ·01	Not significant; $SE_m = \pm 0{\cdot}0015$
Maize	·36± ·01	·40± ·06	·36± ·01	Not significant; $SE_m = \pm 0{\cdot}0310$
Guar ..	·32± ·06	·39± ·10	·31± ·02	Not significant; $SE_m = \pm 0{\cdot}0060$
	Organic nitrogen (gm. % on moisture-free basis)			
Wheat	·053± ·004	·048± ·001	·049± ·001	Not significant; $SE_m = \pm 0{\cdot}1600$
Berseem	·053± ·001	·047± ·001	·047± ·001	Significant at 1% C.D. $= \pm 0{\cdot}0009$
Maize	·062± ·002	·050± ·002	·053± ·002	Significant at 1% C.D. $= \pm 0{\cdot}0039$
Guar ..	·047± ·000	·049± ·001	·048± ·001	Not significant; $SE_m = \pm 0{\cdot}0009$
	pH			
Wheat	7·7 ±0·3	7·9 ±0·3	8·0 ±0·1	Not significant; $SE_m = \pm 0{\cdot}156$
Berseem	8·0 ±0·1	8·0 ±0·0	8·1 ±0·1	Not significant; $SE_m = \pm 0{\cdot}071$
Maize	8·0 ±0·1	8·1 ±0·2	8·2 ±0·1	Not significant; $SE_m = \pm 0{\cdot}014$
Guar ..	7·9 ±0·1	8·2 ±0·2	8·1 ±0·1	Not significant; $SE_m = \pm 0{\cdot}109$

good stand of the crops supported a higher count of the organism than a poor stand of the crop. It was quite possible that the crop was benefited by the presence of the larger number of the organism in the rhizosphere. As compared to wheat and *guar*, berseem and maize were known to be heavy crops. The excretions from roots of these crops might be sufficiently large to support the large population of *Azotobacter* in the rhizosphere. These excretions had apparently induced or caused some changes in the nitrogen

fixing capacity of the organism. Wheat plant apparently had not affected the nitrogen fixing capacity. In the rhizosphere of berseem plant the organism had larger nitrogen fixing capacity than that outside the rhizosphere. In the case of maize, though the organism in the rhizosphere of good maize had higher nitrogen fixing capacity than the organism from the bare soil, there was no difference in the nitrogen fixing capacity of the organism in the rhizosphere of good or bad maize. The excretions from plants showing stunted growth might not be as effective as from vigorously growing plants. The nitrogen fixing capacity of the organism collected from the rhizosphere and non-rhizosphere soils from the *guar* fields also showed the same tendency as those from the maize fields though no difference was noted in their numbers.

From the data in Table II, it was observed that the organic carbon contents and pH value in the rhizosphere soil from good or bad growth of the plant in the fields under any crop were not significantly different from those in the root-free soil. But differences were exhibited in their nitrogen contents. These were particularly interesting in relation to the distribution of the organism and its nitrogen fixing capacity. In the wheat field, no difference between rhizosphere and non-rhizosphere soils was observed either in the numbers of *Azotobacter*, its nitrogen fixing capacity, or in their nitrogen contents. In the berseem fields, the rhizosphere of the crop under a good stand held a large number of *Azotobacter* with high nitrogen fixing capacity, and the soil contained higher nitrogen content. In the fields of maize also, the rhizosphere soil of a good stand of maize contained a higher number of *Azotobacter* with a higher capacity of nitrogen fixation than the bare soil or rhizosphere soil under a bad stand of maize and it contained a larger nitrogen content which might be of some benefit to the crop. In the fields of *guar* there was no difference between the rhizosphere and non-rhizosphere soils in their counts of *Azotobacter* and no difference was observed between them in their nitrogen contents, in spite of the higher nitrogen fixing capacity of the organism in the rhizosphere soil under a good stand of the crop. This might be due to lack of sufficient amounts of energy materials in the form of excretions or degenerated tissues of the root matter from the plants.

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MORPHOLOGY OF THE HEAD CAPSULE AND ITS APPENDAGES OF *ORTHETRUM TAENIOLATUM* SCHNEIDER (ODONATA, ANISOPTERA, LIBELLULIDÆ, LIBELLULINÆ)

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1. INTRODUCTION

THE literature reveals a large number of publications on the morphology of the head of Odonata by foreign authors of which the important ones are by Lew (1934), Sokal (1947), Mittelstaedt (1950) and Short (1955). Of the

various authors who have studied the individual parts of the head, the publications of Imhof (1901) on antennæ, of Taborsky (1927), Munsheid (1933), Butler (1934), Jeannel (1949), Weber (1949) and Strenger (1952) on mouth parts and of Hudson (1948) on tentorium, are also worth mentioning. The only contribution to the knowledge of the morphology of the head of Odonata from India is by Mathur (1956), who studied the head of *Brachythemis contaminata*. In spite of these publications the interpretations regarding some of the structures of the head are not clear. With this view the present authors have studied the head of *Orthetrum tæniolatum* Schneider, a commonly available species of Ajmer.

2. MATERIAL AND METHOD

Adult specimens were locally collected from the neighbourhood of Foy Sagar Lake (Ajmer) and from Happy Valley (Ajmer, 1581 M.S.L.) during the months of September and October. They were identified with the help of *The Fauna of British India*, Vol. III (Fraser, 1936), as *Orthetrum tæniolatum* Schneider. The specimens were preserved in 10% solution of formalin. The head capsules were made transparent by treating with 15% solution of potassium hydroxide at room temperature for 4–5 days. They were subsequently stained in 1% solution of picro-indigo-carmine.

3. HEAD CAPSULE

The head capsule is broader than long and occupies a vertical position in front of the thorax. The caudal aspect is circular and concave. The mouth parts are hypognathous.

(i) *Sutures of the Head Capsule*

(*a*) *Epicranial suture.*—The coronal suture could not be traced. A suture on each side originates near the ventral margin of the median ocellus and runs along the cephalodorsal border of the frons to terminate near its lateral corner. It is in the form of a semicircular suture around the base of antenna. These sutures are considered here as the frontal sutures as they terminate near the bases of antennæ. Sokal (1947) has described three sclerotizations in *Pantala* arising on the ventral side of the median ocellus and has named them as frontal sutures. Regarding the nature of first and second sclerotizations the present authors are not in agreement with Sokal (1947). These sclerotizations terminate far apart from the antennal bases, a criterion by which the frontal sutures are identified here. Moreover, splitting of a suture into two or three parts has not been reported in any species.

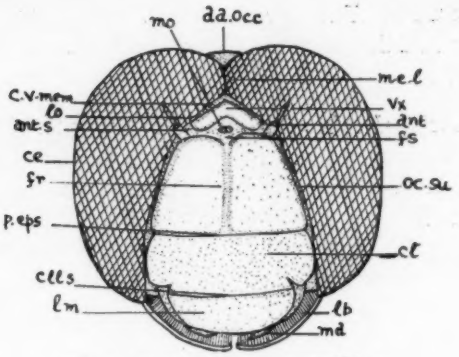

FIG. 1. Cephalic view of the head.

These sclerotizations more probably represent secondary cuticular inflections to support the verticofrontal angle or fastigium, which has been put to extra tension because of the outward bulging of frons and vertex.

(*b*) *Occipital suture.*—The presence of an occipital suture in the adult members of Anisoptera has been denied by all workers except Short (1955) who described a well-developed suture in *Aeshna cyanea.* The temporal sclerotizations described by Sokal (1947) correspond to the occipital suture of Short (1955) in position. The occipital suture is absent in *Orthetrum tæniolatum.*

Lew (1934) maintained that the ocular apodemes are formed by the contribution of the frons, occiput and gena. Sokal (1947) did not agree with such an origin of the ocular apodemes but believed that these sclerites have indistinguishably fused in certain places with the ocular apodemes. However, both of them agree that the occiput extends up to the ocular apodemes. Keeping this point in view it can be said that the occipital suture has merged with the ocular suture in *Orthetrum tæniolatum.*

(*c*) *Postoccipital suture.*—Postoccipital suture is present on the caudal aspect of the head. It starts in a line with the hypostomal suture from the ventral side of a deeply sclerotized area on the occiput. The dorsal termination of the hypostomal suture and the ventral termination of the postoccipital suture are so close in the material under study that the latter suture seems to be in continuation with the former. But a close examination reveals a small area between these two points without a ridge on its ental aspect. This area separates the two sutures. The postoccipital suture runs dorsomesad and when it reaches half the length of the foramen magnum turns inwards making an angle of 130°. It ends near the dorsal

corner of the foramen. The two sutures of the opposite sides unite with each other in the middle above the foramen magnum, the union being only faintly discernible.

(*d*) *Caudal occipital sclerotizations.*—One sclerotization, radiating dorsolaterally from the angle where the postoccipital suture bends at 130°, has been noticed on each side. Various authors have described these sutures under different names as, occipital process (Lew, 1934), occipito-postgenal suture (Mathur, 1956) and caudal occipital sclerotization (Sokal, 1947). The sclerotizations become obsolete after traversing a little distance in the

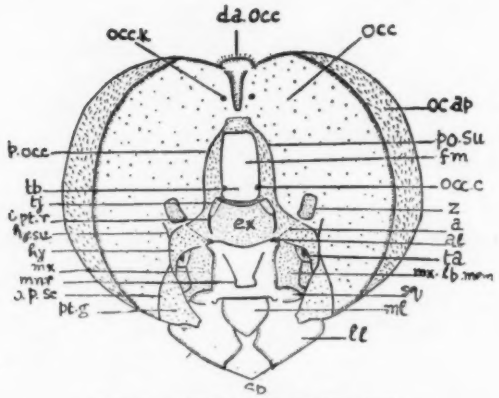

FIG. 2. Caudal view of the head.

occiput in *Orthetrum tæniolatum*. The present authors are not able to subscribe to Mathur's (1956) interpretation of this sclerotization as occipito-postgenal suture, which seems to be based on the erroneous assumption that the ventral boundary of the occiput is formed by this sclerotization. The occiput is the area between occipital and postoccipital sutures (Snodgrass, 1935). In the species under study the lateral limits of the occiput are bounded by ocular apodemes since the occipital suture has merged with the former. In such cases the occiput is the area between postoccipital suture and ocular apodemes. The sclerotizations in question are placed far dorsal to the ventral termination of the postoccipital suture and as such do not bound the postocciput ventrally but simply lie in the latter. The present authors agree with Sokal (1947) and Lew (1934) that these sclerotizations only support the over-enlarged occiput.

(*e*) *Epistomal suture.*—The transverse line separating the frons and clypeus in the ectal aspect is termed by Short (1955) and Mathur (1956) as

the epistomal suture. The suture-like transverse line is formed by the abutting of the margins (which are formed by the inward turning of the frons and clypeus) of frons and clypeus. Sokal (1947) has correctly termed this line as the psuedoepistomal suture. It turns cephalolaterally and then mesally to join with epistomal suture near the anterior mandibular articulations. The epistomal suture lies below this line and merges with the epistomal ridge to which are attached the anterior margin of frons and posterior margin of clypeus. The epistomal ridge is a mechanical device to give rigidity against the cutting action of the mandibles.

(*f*) *Ocular sutures.*—Each compound eye is surrounded by an ocular suture. The two sutures unite with each other on the dorsal meson forming the median eyeline. In the cephalic view the ocular sutures have the appearance of a big inverted 'Y' with the vertex, frons, clypeus and genæ between its diverging arms while the stalk of 'Y' represents the median eyeline. Internally, the ocular sutures bear well developed apodemes, the ocular apodemes.

(*g*) *Subgenal sutures.*—The pleurostomal suture (Snodgrass, 1935) starts near the anterior mandibular articulation in the form of a sclerotized line to terminate near the posterior mandibular articulation. From the posterior mandibular articulation another suture, the hypostomal suture (Snodgrass, 1935), starts which courses laterad and caudad. It ascends to the caudal side of the head. Slightly above the articulation of maxilla with the hypostoma it curves and ends near the ventral side of the sclerotized point on the occiput. It is not bifurcated in *Orthetrum tæniolatum.*

(*h*) *Occipito-postgenal sclerotization.*—A faint sclerotization originating near the dorsal level of the mandibular articular protuberance is observed for the first time in Odonata by the present authors. On each side it courses dorsomesad and unites with the hypostomal suture. It runs with the latter for some distance and then deviates from it, giving the hypostomal suture a bifurcated appearance. After separating the sclerotization runs dorsad and laterad to the sclerotized area (stridulating organ of Berlese, 1909). The present authors consider that this sclerotization separates a small triangular area, the postgena, from the occiput. The postgena is sunken in as compared with the occiput and forms a border with it parallel to the above-mentioned sclerotization.

(ii) *Areas of the Cranium*

(*a*) *The frontoclypeal area.*—The frontoclypeal area exhibits the generalised condition except for the outward bulge. The dorsal and the dorsolateral limits of the frons are not clear because of the peculiar frontal sutures

present here. The dorsolateral limits are determined arbitrarily by a line which separates a rim around the ocular apodemes from the frons. This rim forms a part of the parietals. The frons has a well-defined crest, and is indistinguishably fused with the fastigium dorsally. The part of the frons below the pseudepistomal suture is membranous. The clypeus has been referred to by Sokal (1947) and Mathur (1956) in *Pantala* and *Brachythemis contaminata* respectively as divided transversely by a membranous area into a dorsal postclypeus and a ventral anteclypeus. The clypeus remains undivided in *Orthetrum tæniolatum*. Two chitinous spots marking the position of internal apodemes have been observed on the lateral sides of the posterior region of the ectal aspect of the clypeus. These apodemes give attachment to the cibarial muscles.

(*b*) *The parietals.*—The parietals have undergone many important changes and are represented by circumvertical membrane, antennal sclerite, fastigium, genæ and the rim surrounding the ocular apodemes. Of these parts the attachment of the circumvertical membrane to the vertex, antennal sclerite, fastigium and genæ have attracted attention of the present authors because of a few discrepancies in their interpretations.

(i) *Attachment of the circumvertical membrane to the vertex.*—The vertex seems to be continuous with the circumvertical membrane in the ectal aspect. On the ental aspect the caudal wall of the vertex is seen turned inwards in the form of a wide band, the crescent-shaped lamella. Such a condition can be explained in one of the two ways. Either the circumvertical membrane has been secondarily attached on the vertex dorsad to the crescent-shaped lamella or the crescent-shaped lamella may be considered as an apodeme formed at the junction of vertex and circumvertical membrane. According to the first explanation the crescent-shaped lamella is the incurved part of the vertex, which is more probable.

(ii) *Antennal sclerite.*—The sclerites on the sides of fastigium are continuous dorsally with the circumvertical membrane. Laterally these sclerites are attached to the ocular apodemes and ventrally they bulge out to unite with the frons. From the ventral sides of these sclerites arise the antennæ. Sokal (1947) termed these sclerites as parafrons. Short (1955), while describing the morphology of the head of *Aeshna cyanea*, has labelled this area in his Fig. 4 *a*, p. 208, as ' osc ' which he has not explained. The present authors consider this sclerite as antennal sclerite, since the antennæ are attached to it.

(iii) *Verticofrontal angle or fastigium.*—Mathur (1956) has labelled the angle between the frons and vertex as frontal suture and its ental aspect

as frontal ridge. He, however, confuses a previously clear situation by considering the angle as a whole a suture. He seems to have confused Sokal's (1947) interpretation of frontal suture as three sclerotizations of which two are situated in this angle. When the frontal sutures are completed at their mesial ends this area (verticofrontal angle) is separated from the frons. According to Snodgrass (1935) fastigium forms a part of the parietals. It has a ridge-like appearance on the ental aspect. Dorsal to the median ocellus entally a flap-like projection comes out from the fastigium, the sheath of median ocellus. One verticofrontal apodeme arises from either side of the fastigium. These apodemes project into the cranial cavity and serve for the attachment of the labral muscles.

(iv) *Genæ*.—The genæ are pushed under the frontoclypeus by the development of the compound eyes. Dorsomesally it is continuous with the frons. The frontogenal sutures are absent and, therefore, the frontal limit of the gena is arbitrarily defined as the line along which the frons reflect to form the gena. Mesally it is indistinguishably fused with the anterior tentorial arms.

(*c*) *Occipital arch*.—The occiput occupies dorsal and caudal aspects of the head. The caudal part is broad and concave, limited ventrally by occipito-postgenal sclerotization. It has two pairs of darkly sclerotized points. First pair, the occipital knobs, is situated dorsocaudad. They are formed by the fusion of the ocular apodemes with the ental aspect of the caudal part of the occiput. The occipital knobs increase the rigidity of the head capsule. The second pair lies dorsal to the dorsal termination of the hypostomal suture and the ventral termination of the postoccipital suture. A broad anteriorly pointed lobe, protruding from the prothorax, touches this area. Berlese (1909) considered that such an arrangement is for the production of sound. His view is not tenable because of the absence of the true auditory organs in dragonflies and that no worker on Odonata has reported dragonflies stridulating. This arrangement is believed to give an extra attachment to the head with neck.

(*d*) *Postgena*.—Some authors have described the ventral part of the occiput and the part mesal to the hypostomal suture as subgena while others described this part as postgena. The present authors are of the opinion that the part mesal to the hypostomal suture is the subgenal area (the hypostoma), while the area outside this suture bounded dorsally by the occipito-postgenal sclerotization and laterally by the ocular apodemes is the postgena. The postgena also takes part in the formation of the mandibular articular protuberance.

(*e*) *Postocciput.*—The postocciput is sunken in and surrounds the foramen magnum dorsally by a narrow stripe and laterally by a triangular piece. It is peculiar that the postocciput extends to the ventral side of the foramen also as a narrow stripe up to the basal labial articulations which mark the position of the posterior tentorial pits. It is separated from the hypostoma by a hypothetical line which joins the ventral tip of the occipito-postgenal border and the basal labial articulation. Slightly above the tentorial bridge the postocciput projects in the form of two chitinous outgrowths, the occipital condyles. These condyles give attachment to the cervical sclerites.

(*f*) *A membranous area is present between the labial articulations and tentorial bridge.*—It is bounded laterally by the mesal boundary of the post-occiput lying ventral to the foramen magnum. This area has been termed by Sokal (1947) as gular membrane. Marshall (1914) and Mathur (1956) consider it to be membranous gula and the latter author compares it with the membranous gula of certain larval Coleoptera. The presence of gula is generally associated with the prognathous condition and is not expected in dragonflies having the hypognathous condition. When the specimens not treated with potassium hydroxide are examined with the neck *in situ* it is observed that the membranous area is an extension of the neck membrane.

(*g*) *Subgenal areas.*—The pleurostomal and the hypostomal segments of the subgenal sutures bound the pleurostoma and hypostoma respectively. The former is much reduced and membranous. It is attached to the base of the mandibles. The hypostoma is much chitinized and bears a cup for the articulation of maxilla. From the former projects a triangular area which fits into the concavity of the juxtacardo.

4. ANTENNÆ

The antennæ are inconspicuous and are attached to the dorsolateral margins of the frons on the antennal sclerites. Each antenna is lodged in a small cavity, the antacava (Stickney, 1923) or antennal socket (Snodgrass, 1935). The antacava is surrounded by a narrow ridge. The present authors fail to recognise the presence of an antennal suture of Crampton (1921) and Snodgrass (1935). The base of antenna is attached to a circular elastic membrane, the antacorium, which helps in the free movement of the former (Khatib, 1946). The scape and pedicel are thick, the flagellum is bristle-like and tapers to the distal end. The scape narrows at the proximal end and is attached with the antacorium directly. Distally the scape becomes broader and has an articular cup. The pedicel fits in the cup by a

more chitinised area. It is longer than the scape. Flagellum is four-segmented and each segment articulates by a ball and socket arrangement. The first segment is the longest, the second and third are equal, while the fourth is longer than the second and third but shorter than the first. The distal segment of the flagellum has a rounded end.

5. Tentorium

Tentorium is well developed and chitinous. It is ⅄-shaped, a characteristic feature of Odonata. There is no trace of the posterior tentorial pits in *Orthetrum tæniolatum*. Each posterior tentorial arm is reduced and is represented by a ridge situated mesad to the hypothetical line which separates the hypostoma from postocciput. This ridge is attached to the tentorial junction. Hudson (1948) and Mathur (1956) have called the tentorial junction as the posterior tentorial arm. The junction is actually formed by the chitinization of the parts of dorsal and anterior tentorial arms. The anterior tentorial arms broaden distally to open on the dorsal wall of the head by means of anterior tentorial pits. The latter are situated on the lateral parts of the epistomal ridge and throughout the length of the pleurostomal suture. Such a condition is more primitive than that found in Orthopteroids (Hudson, 1948). The epistomal part of the anterior tentorial arm makes a clockwise turn before it reaches the tentorial junction. Two tendons are given out from the anterior tentorial arm. The proximal tendon, the mandibular process, arises from the tentorial junction. It is delicate and its distal end is rounded. The distal tendon, the maxillary process, arising from the ventral side of the epistomal part of anterior tentorial arm, is a heavy projection with a broadly flattened end. The dorsal arms are well developed and arise along short lines from the dorsal sides of the anterior tentorial arms. Each dorsal arm has a pit in the form of a suture above the antennal base. The tentorial junctions are connected by a bridge which exhibits a caudad bent. To this bridge are attached the circumcervical sclerites.

6. Mouth Parts

(i) *Labrum*

The labrum is composed of two walls apposed at the margins. Its free border is semicircular and beset with long setæ. The caudal wall is divided into two regions, a lateral sclerotized area and a mesal unpigmented membranous area. The mesal area bears the gustatory papillæ and sensillæ. Three sclerotized points, one median and two lateral, are present in this area for the attachment of the labral muscles. Tillyard (1917) and

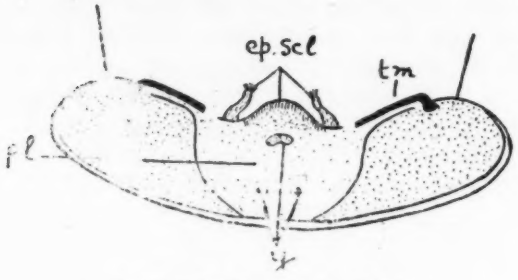

FIG. 3. Caudal view of labrum.

Mathur (1956) have committed the same mistake as that of Comstock and Kellogg (1904), Packard (1909), Yuasa (1927) and Imms (1951) by using the term 'epipharynx' for the caudal wall of the labrum. Cook (1944) has rightly suggested the term 'palatum' for the inner surface of the labrum or the dorsal wall of the cibarium, as the original usage of the term 'epipharynx' was for the membranous lobe on the dorsal surface of the preoral cavity.

There are two heavy dark projections of chitin at the base of the caudal wall of the labrum. Between them is a conical protuberance not as high as its companions and less chitinized than them. Taborsky (1927) has named them as 'epipharyngeal sclerites'. The lateral chitinizations are covered with many stiff setæ giving it a brush-like appearance.

(ii) *Mandibles*

The mandibles are situated on the lateral margins of the preoral cavity. They are directed forwards and inwards. The right mandible is longer than the left. Each mandible articulates with the head at two points. Anteriorly it has a cup-like cavity into which fits the articular knob of the clypeus. Posterior articular condyle of the mandible is well developed and fits in the cup of the mandibular protuberance. The cutting margin of each mandible bears teeth differentiated into three incisors and one molar. The first incisor is a long pointed tooth, the second lying behind the first is a small tooth. The third incisor lies in the same plane as the first. The incisors are single cuspid. The molar is formed of four teeth arranged at the corners of 'Z' forming a four cuspid molar. Because of the arrangement the first and the third molar teeth lie in the same plane, while second and fourth in another. The first tooth is the broadest and the third is the longest.

At the base of the mandibles are attached two large apodemes, the inner broad adductor and the outer narrow abductor for the insertion of adductor

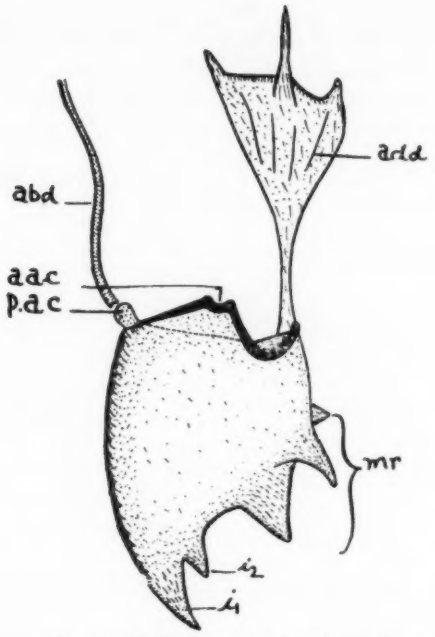

FIG. 4. Cephalic view of left mandible.

and abductor muscles respectively. The mandible represents a primitive condition in having both tentorial and hypopharyngeal adductors and cranial abductor and adductor.

(iii) *Maxillæ*

Each maxilla is situated on the caudal side of the head beneath the mandible, on either side of the mesally placed labium. It is attached to the hypostoma by a curved process of its proximal segment.

Cardo.—This is the proximal part of maxilla. It is divided into two parts, juxtacardo and veracardo (Crampton, 1916). The cardo is placed at an angle with the second segment of the maxilla, the stipes. The veracardo is formed of two folds united dorsally. It forms a much sclerotized curved process anteriorly which bears a thin slender apodeme, the promotor apodeme of veracardo. The juxtacardo is attached to the cepahlic fold of the veracardo and projects beyond it. The projected part is flat and much chitinized. It has a concavity into which the triangular projection from the hypostoma fits.

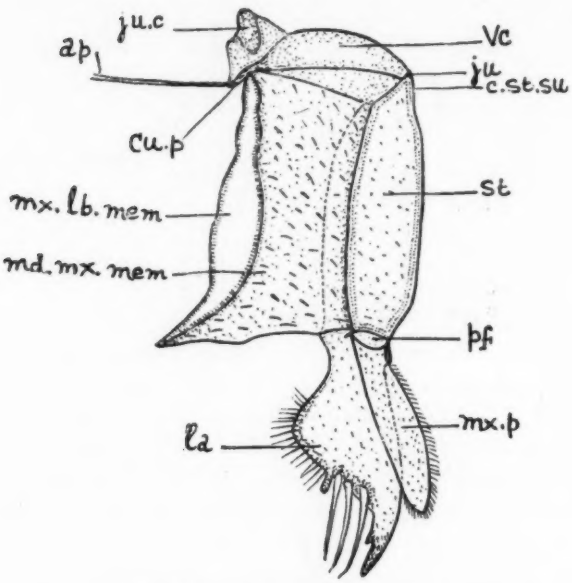

FIG. 5. Cephalic view of left maxilla.

Stipes.—The stipes is unsegmented and formed of two folds united to give an appearance of a boat. It is separated from the cardo by a cardo-stipital suture having internally a ridge. The cardostipital apodeme is absent. The stipes bears an inner and outer lobe at its distal margin. There are various views on the formation of the inner lobe. Berlese (1909), Tillyard (1917) and Jeannel (1949) maintained that the inner lobe represents the fused galea and lacinia. Weber (1949) on the contrary considers it as the lacinia only, the galea being absent. Imms (1951) has called the single inner lobe as a mala. Strenger (1952) has given an entirely different view. According to him the maxillary palp is absent and the inner and outer lobes represent the lacinia and galea respectively. The present authors consider the outer lobe as the maxillary palp and the inner as the lacinia. The proximal portion of the lacinia is swollen and bears six incurved spines. Three of these spines lie in one plane and the rest three in another. Out of the three on the cephalic end, the first is pointed and long while the second is pointed and short. The third spine is short and blunt in the left maxilla but pointed and long in the right one. The rest three have their origin on the lacinia slightly mesad to its inner margin. These are long and pointed except the last which is slightly shorter. At the base of the maxillary palp and separated from the stipes there is a small segment, the palpifer.

(iv) *Labium*

The labium is attached to the postocciput by two long pointed and much sclerotized articular processes. Each articular process is placed slightly mesal to the lateral side of the proximal part of the labium. Butler (1904), Lucas (1922), Whedon (1927) and Mathur (1956) have divided the labium

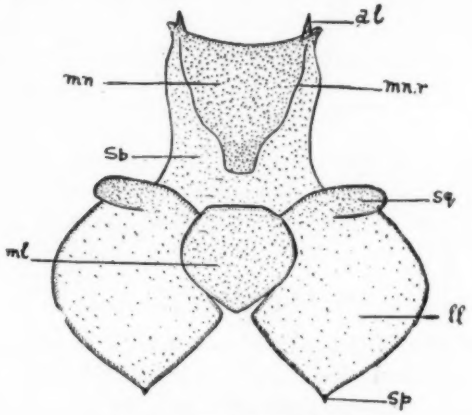

FIG. 6. Aboral view of labium.

into three segments, the submentum, the mentum and the terminal segment. Short (1955) and Corbet (1951, 1953), however, divide the labium into two parts, prelabium and postlabium. The present authors divide the labium into three parts because of the presence of the submento-mental muscles and the insertion of the adductors of the lateral lobes on the mental ridge. The submentum is separated from the mentum by a well-defined mental ridge. The mentum is more chitinized than the submentum and bears paired squamme to which are attached the lateral lobes. The median lobe is directly attached to the mentum. The lateral lobes have been homologized with the labial palp and the median lobe with the fused lacinia and galea by Butler (1904).

(v) *Hypopharynx*

The well-developed double-walled hypopharynx arises from the floor of the mouth cavity and remains adnate to the adoral wall of the labium. The suspensorium is simple and consists of two long lateral rods on the proximal part of the hypopharynx. On the sides of the mouth-opening there are lateral projections which bear long, distally broaden, apodemes for the hypopharyngeal adductor muscles of the mandibles. The aboral wall of the hypopharynx is attached to the adoral wall of the labium and

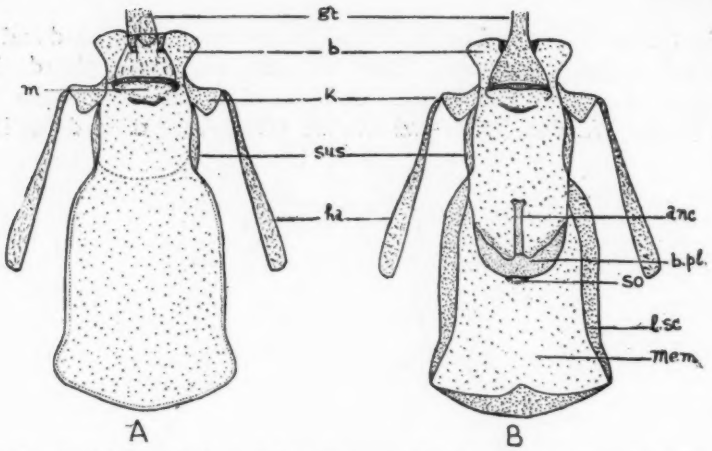

FIG. 7. (*a*) Adoral view of hypopharynx. (*b*) Aboral view of hypopharynx.

forms the salivarium. The proximal side of the aboral wall of the hypopharynx is concave and the margins are considerably sclerotized. The sclerotized band is continuous adorally with the suspensorial bars. It has been homologized with the basal sclerite of the Orthopteroids. Anterior to the basal sclerite lies the salivary orifice. The anchor sclerite (Snodgrass, 1951), a slender apodeme with bifid distal end, arises from the basal sclerite. Short (1955) has misunderstood Snodgrass' (1935) anchor sclerite as the posterior part of the basal sclerite.

7. SUMMARY

The present paper gives a detailed account of the morphology of the head capsule and its appendages of *Orthetrum tæniolatum*. The following features are noteworthy:

1. The coronal suture is absent and the frontal sutures start below the median ocellus.

2. The frons is indistinguishably fused with the fastigium.

3. The occiput is well developed and the occipital suture is absent.

4. The postgena is separated from the occiput by occipito-postgenal sclerotization.

5. The antennæ are inconspicuous and are situated on the ventral side of the antennal sclerites.

6. Tentorium is primitive than that of the Orthopteroids as the anterior tentorial pits are situated in the pleurostomal sutures also.

7. The hypopharynx is well developed and has an anchor sclerite in the adult.

8. There is an extension of the neck membrane attached to the submentum.

9. The postocciput extends to the ventral side of the foramen magnum.

10. The postgena is bounded mesally by the hypostomal suture, dorsally by occipito-postgenal sclerotization and laterally by ocular apodemes.

8. Acknowledgements

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10. Abbreviations

a. .. hypothetical line joining the basal labial articulation and the ventral termination of postoccipital suture.
a.a.c. .. Anterior articular cup of mandible.
abd. .. Abductor apodeme of mandible.
abb. .. Adductor apodeme of mandible.
al. .. Articular process of labium.
ap. .. Promotor apodeme of veracardo.
anc. .. Anchor sclerite.
an. s. .. Antennal sclerite.
ant. .. Antenna.
b. .. Part of membranous area of labrum with epipharyngeal sclerite.
b.pl. .. Basal plate.
c.st.su. .. Cardostipital suture.
ce. .. Compound eye.
cl. .. Clypeus.
clls. .. Clypeolabral suture.
cu.p. .. Curved process.
c.v.mem. .. Circumvertical membrane.
d.a.occ. .. Dorsal aspect of occiput.
ep.scl. .. Epipharyngeal sclerite.
ex. .. Extension of neck membrane.
fr. .. Frons.
fs. .. Fastigium.
fm. .. Foramen magnum.
gt. .. Gut.
ha. .. Apodeme for hypopharyngeal adductor muscle of mandible.
hy. .. Hypostoma.
hy.su. .. Hypostomal suture.
i_1. .. First incisor.
i_2 .. Second incisor.
i.pt.r. .. Impression of posterior tentorial ridge.
ju. .. Juxtacardo.
ju.c. .. Concavity of juxtacardo.
k. .. Lateral projections on the sides of mouth.
la. .. Lacinia.
l_b. .. Labium.
ll. .. Lateral lobe.
lm. .. Labrum.
lo. .. Lateral ocellus.
l.sc. .. Lateral sclerotized area of hypopharynx.
m. .. Mouth.
m.e.l. .. Median eyeline.
md. .. Mandible.
md.mx.mem. .. Mandibulo-maxillar membrane.
mem. .. Median membranous area of hypopharynx.
ml. .. Median lobe.
mn. .. Mentum.
mn.r. .. Mental ridge.
mo. .. Median ocellus.
mr. .. Molars.
mx.lb.mem. .. Maxillo-labral membrane.
mx.p. .. Maxillary palp.
o.p.sc. .. Occipito-postgenal sclerotization.
oc.ap. .. Ocular apodeme.
oc.sc. .. Ocular suture.
occ. .. Occiput.
occ.c .. Occipital condyle.
occ.k. .. Occipital knob.
p.a.c. .. Posterior articular condyle of mandible.
p.eps. .. Pseudoepistomal suture.
p.occ. .. Postocciput.
pf. .. Palpifer.
pl. .. Palatum.
pt.g. .. Postgena.
sb. .. Submentum.
so. .. Salivary orifice.
sp. .. Spine.
sq. .. Squamma.
st. .. Stipes.
sus. .. Suspensorium.
ta. .. Triangular area.
th. .. Tentorial bridge.
tm. .. Torma.
tj. .. Tentorial junction.
vc. .. Veracardo.
vx. .. Vertex.
y. .. Sclerotized area in the membranous region of the caudal wall of labrum.
z. .. Sclerotized area against which lobe of prothorax fits.

STUDIES ON INDIAN ICHNEUMONIDÆ (HYMENOPTERA)

Subfamily: GELINÆ

Part II. Tribe MESOSTENINI

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Tribe 3. MESOSTENINI (= CRYPTINI)

TAXONOMISTS on Ichneumonidæ had divided this tribe into Cryptini and Mesostenini on the single character that in the former the areolet was large and in the latter small. This classification does not stand the test of recent trends in taxonomy. Indeed in many cases related genera are separated

and genera not related at all brought together. In many species the areolet is intermediate in size and it is rather difficult to assign these either to Cryptini or to Mesostenini. We, therefore, are of the opinion that these two tribes should be combined into one with Mesostenini based on the genus *Mesostenus* Grav. which is one of the oldest generic name of the tribe. Gravenhorst proposed several other names of equal age but we agree with Townes in the use of the name *Mesostenus* as this name was first used as the basis for super-generic group name.

Ichneumon parasites belonging to this tribe are parasitic on larvæ, pre-pupæ and pupæ of Lepidoptera, Symphata and Aculeata of Hymenoptera and eggs of spiders of order Araneida.

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Cryptini (Tribe 4) Ashmead, *Proc. ent. Soc. Wash.*, **3**: 278, (1874).

Schmiede-Knecht, *Genera Insect.*, fas. **75**: 3, (1908). Townes, *Mem. Amer. ent. Soc.*, **11** (1): 251, (1944).

Cryptides (Tribe) Morley, *Ichn. Brit.*, **2**: 1, (1906).

Mesostenini Ashmead, *Smith's Insect of New Jersey*, p. 570, (1900).

Schmiede-Knecht, *Genera Insect.*, fas. **75**: 45, (1908).

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ACRORICNUS Ratzeburg

Acroricnus Ratzeburg, *Ichn. d. Forstins.*, **3**: 92, (1853), (Type of genus: *Acroricnus schaumii* Ratzeburg). Schmiede-Knecht, *Genera Insect.*, fas. **75**: 13, (1908). Morley, *Ichn. Brit.*, **2**: 324, (1906). Dutt, *Mem. Dep. Agric. India Ent.*, **8** (2): 22, (1923). Townes, *Mem. Amer. ent. Soc.*, **11** (1): 296, (1944). Muesebeck, Krombein, Townes and others, *U.S. Dep. Agric. Monograph*, **2**: 275, (1951).

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Macrobatus Holmgren, *Svenska Vet. Akad. Handl.*, **75**: 50, (1856). Schmiede-Knecht, *Genera Insect.*, fas. **75**: 13, (1908). Townes, *Mem. Amer. ent. Soc.*, **11** (1): 296, (1944). Muesebeck, Krombein, Townes and others, *U.S. Dep Agric. Monograph*, **2**: 275, (1951).

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peronatus Cameron

Acroricnus peronatus Cameron, *The Entomologist*, p. 182, (1903). ♀[1]. Schmiede-Knecht, *Genera Insect.*, fas. **75**: 14, (1908). Dutt, *Mem. Dep. Agric. India, Ent.*, **8** (2): 22, (1923).[2]

[1] India.
[2] Punjab: Simla.

ETHA Cameron

Etha Cameron, *Mem. and Proc. Manchester Lit. Philos. Soc.*, **47**: 17, (1903),[1] (Type of genus: *E. striatifrons* Cam). Schmiede-Knecht, *Genera Insect.*, fas. **75**: 16, (1908).

[1] Assam: Khasia Hills.

dentata Cameron

Etha dentata Cameron, *Mem. and Proc. Manchester Lit. Philos. Soc.*, **47**: 26, (1903). ♂[1]. Schmiede-Knecht, *Genera Insect.*, fas. **75**: 16, (1908).

[1] Khasia Hills.

fusciventris Cameron

Etha fusciventris Cameron, *Mem. and Proc. Manchester Lit. Philos. Soc.*, **47**: 22, (1903). ♀.[1] Schmiede-Knecht, *Genera Insect.*, fas. **75**: 16, (1908).

[1] Khasia Hills.

khasiana Cameron

Etha khasiana Cameron, *Trans. ent. Soc. Lond.*, p. 103, (1904), ♀.[1] Schmiede-Knecht, *Genera Insect.*, fas. **75**: 16, (1908).

[1] Khasia Hills.

lacteiventris Cameron

Etha lacteiventris Cameron, *Trans. ent. Soc. Lond.*, p. 103, (1904). ♀.[1] Schmiede-Knecht, *Genera Insect.*, fas. **75**: 16, (1908).

[1] Khasia Hills.

lævifrons Cameron

Etha lævifrons Cameron, *Mem. and Proc. Manchester Lit. Philos. Soc.*, **47**: 20, (1903). ♀.[1] Schmiede-Knecht, *Genera Insect.*, fas. **75**: 16, (1908). [1] Khasia Hills.

plumbea Cameron

Etha plumbea Cameron, *Mem and. Proc. Manchester, Lit. Philos. Soc.*, **47**: 21, (1903). ♂.[1] Schmiede-Knecht, *Genera Insect.*, fas. **75**: 16, (1908). [1] Khasia Hills.

rufofermorata Cameron

Etha rufofermorata Cameron, *Mem. and Proc. Manchester Lit. Philos. Soc.*, **47**: 28, (1903). ♂.[1] Schmiede-Knecht, *Genera Insect.*, fas. **75**: 16, (1908). [1] Khasia Hills.

striatifrons Cameron

Etha striatifrons Cameron, *Mem. and Proc. Manchester Lit. Philos. Soc.*, **47**: 18, (1903). ♀.[1] Schmiede-Knecht, *Genera Insect.*, fas. **75**: 16, (1908). [1] Khasia Hills.

testaceipes Cameron

Etha testaceipes Cameron, *Mem. and Proc. Manchester Lit. Philos. Soc.*, **47**: 24, (1903). ♀.[1] Schmiede-Knecht, *Genera Insect.*, fas. **75**: 16, (1908). [1] Khasia Hills.

BATHYCRISIS Cameron

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striaticollis Cameron

Bathycrisis striaticollis Cameron, *Spolia zeylan.*, **3**: 97, (1905). ♂.[1] Schmiede-Knecht, *Genera Insect.*, fas. **75**: 17, (1908). [1] Ceylon: Trincomali.

HADROCRYPTUS Cameron

Hadrocryptus Cameron, *Mem. and Proc. Manchester Lit. Philos. Soc.*, **47**: 11, (1903), (Type of genus: *H. nasutus* Cameron). Schmiede-Knecht, *Genera Insect.*, fas. **75**: 19, (1908). Dutt, *Mem. Dep. Agric. India, Ent.*, **8** (2): 22, (1923).

nasutus Cameron

Hadrocryptus nasutus Cameron, *Mem. and Proc. Manchester Lit. Philos. Soc.*, **47**: 12, (1903). ♀.[1] Schmiede-Knecht, *Genera Insect.*, fas. **75**: 20, (1908).

[1] Khasia Hills.

postfurcalis Morley M. S.

Hadrocryptus postfurcalis Dutt, *Mem. Dep. Agric. India, Ent.*, **8** (2): 22, (1923).[1]

[1] Bombay: Belgaum.

triangularis Morley M.S.

Hadrocryptus triangularis Dutt, *Mem. Dep. Agric. India, Ent.*, **8** (2): 22, (1923).[1]

[1] Bihar: Chapra.

tuberculatus Cameron

Hadrocryptus tuberculatus Cameron, *The Entomologist*, **40**: 5.[1]

[1] Bhotan.

COMPSOCRYPTUS Ashmead

Cryptoideus Ashmead, *Proc. U.S. Nat. Mus.*, **23**: 42, (1900). Muesebeck, Krombein, Townes and others, *U.S. Dep. Agric. Monograph*, 2: 263, (1951).

Compsocryptus Ashmead, *Proc. U.S. Nat. Mus.*, **23**: 431, (1900), (Type of genus: *Cryptus calipterus* Say). Schmiede-Knecht, *Genera Insect.*, fas. **75**: 20, (1908). Muesebeck, Krombein, Townes and others, *U.S. Dep. Agric. Monograph*, **2**: 263, (1951).

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others, *U.S. Dep. Agric. Monograph*, **2**: 263, (1951).

Stictocryptus Cameron, *Zeit. Syst. Hymen. Dipt.*, **7**: 462, (1907). Dutt, *Mem. Dep. Agric. India, Ent.*, **8** (2): 24, (1923). Muesebeck, Krombein, Townes and others, *U.S. Dep. Agric. Monograph*, **2**: 263, (1951).

dentifrons (Morley), n. comb.

Stictocryptus dentifrons Dutt, *Mem. Dep. Agric. India, Ent.*, **8** (2): 24, (1923).[1] [1] Bihar: Chapra.

testaceous (Cameron), n. comb.

Stictocryptus testaceous Cameron, *Zeit. Syst. Hymen. Dipt.*, **7**: 462, (1907). ♂. Dutt, *Mem. Dep. Agric. India, Ent.*, **8** (2): 25, (1923).[1] [1] Bihar: Chapra. Madras: Coimbatore.

PLESIOCRYPTUS Cameron

Plesiocryptus Cameron, *Zeits. f. Hymen. Dipt.*, **5**: 299, (1903), (Type of genus: *P. carinifrons* Cameron). Schmiede-Knecht, *Genera Insect.*, fas. **75**: 21, (1908). Dutt, *Mem. Dep. Agric. India, Ent.*, **8** (2): 22, (1923).

carinifrons Cameron

Plesiocryptus carinifrons Cameron, *Zeits. f. Hymen. Dep.*, **5**: 300, (1903). ♀.[1] Schmiede-Knecht, *Genera Insect.*, fas. **75**: 21, (1908). Dutt, *Mem. Dep. Agric. India, Ent.*, **8** (2): 22, (1923).[2] [1] Punjab: Simla. [2] Punjab: Murree 7,500 ft.

TRACHYSPHYRUS Haliday

Cryptus Fabricius, *Syst. Piez.*, p. 70, (1804). Preocc., Dalla Torre, *Cat. Hymen.*, **3**: 558, (1901–02). Morley, *Ich. Brit.*, **2**: 301, (1906). Schmiede-Knecht, *Genera Insect.*, fas. **75**: 22, (1908). Dutt, *Mem. Dep. Agric. India, Ent.*, **8** (2): 22, (1923). Townes, *Mem. Amer. ent. Soc.*, **11** (1): 274, (1944). Muesebeck, Krombein, Townes and others, *U.S. Dep. Agric. Monograph*, **2**: 259, (1951).

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Meringopus Forster, *Verh. Naturh. Ver. Rheinl.*, **25**: 186, (1868). Townes, *Mem. Amer. ent. Soc.*, **11** (1): 275, (1944). Muesebeck, Krombein, Townes and others, *U.S. Dep. Agric. Monograph*, **2**: 259, (1951.)

Itamoplex Forster, *Verh. Naturh. Ver. Rheinl.*, **25**: 188, (1868). Townes, *Mem. Amer. ent. Soc.*, **11** (1): 275, (1944). Muesebeck, Krombein, Townes and others, *U.S. Dep. Agric. Monograph*, **2**: 259, (1951).

Goniocryptus Thomson, *Opusc. ent.*, fas. **5**: 471, 490, (1873). Townes, *Mem. Amer. ent. Soc.*, **11** (1): 275, (1944). Muesebeck, Krombein, Townes and others, *U.S. Dep. Agric. Monograph*, **2**: 259, (1951).

Hedycryptus Cameron, *Zeit. System. Hymen. Dipt.*, **3**: 298, (1903). Schmiede-Knecht, *Genera Insect.*, fas. **75**: 22, (1908). Townes, *Mem. Amer. ent. Soc.*, **11** (1): 275, (1944). Muesebeck, Krombein, Townes and others, *U.S. Dep. Agric. Monograph*, **2**: 259, (1951).

Cyanocryptus Cameron, *The Entomologist*, **36**: 121, (1903). Townes, *Mem. Amer. ent. Soc.*, **11** (1): 275, (1944). Muesebeck, Krombein, Townes and others, *U.S. Dep. Agric. Monograph*, **2**: 259, (1951).

Steriphocryptus Cameron, *The Entomologist*, **36**: 233, (1903). Schmiede-Knecht, *Genera Insect.*, fas. **75**: 22, (1908), Townes, *Mem. Amer. ent.*

Soc., **11** (1): 275, (1944). Muesebeck, Krombein, Townes and others, *U.S. Dep. Agric. Monograph*, **2**: 259, (1951).

Lamprocryptus Cameron, *Amer. ent. Soc. Trans.*, **35**: 435–36, (1910). Preocc. Townes, *Mem. Amer. ent. Soc.*, **11** (1): 275, (1944). Muesebeck, Krombein, Townes and others, *U.S. Dep. Agric. Monograph*, **2**: 259, (1951).

bibulcus (Cameron), n. comb.

Cryptus bibulcus Cameron, *Trans. ent. Soc. Lond.*, p. 106, (1904). ♂.[1] Schmiede-Knecht, *Genera Insect.*, fas. **75**: 23, (1908). [1] Assam.

excavatus (Cameron), n. comb.

Cryptus excavatus Cameron, *The Entomologist*, p. 84, (1905). ♀.[1] Schmiede-Knecht, *Genera Insect.*, fas. **75**: 25, (1908). [1] India: Simla.

filicornis (Cameron), n. comb.

Hedycryptus filicornis Cameron, *Zeit. System. Hymen. Dipt.*, **3**: 299, (1903). ♀.[1] Schmiede-Knecht, *Genera Insect.*, fas. **75**: 26, (1908). [1] India.

himalayensis (Cameron), n. comb.

Cryptus himalayensis Cameron, *Trans. ent. Soc. Lond.*, p. 106, (1904).[1] Schmiede-Knecht, *Genera Insect.*, fas. **75**: 26, (1908). [1] India: Assam.

indicus (Cameron), n. comb.

Cryptus indicus Cameron, *Mem. and Proc. Manchester Lit. Philos. Soc.*, **41**: 14, (1897).[1] Schmiede-Knecht, *Genera Insect.*, fas. **75**: 27, (1908). [1] India.

infernalis (Cameron), n. comb.

Cryptus infernalis Cameron, *Mem. and Proc. Manchester Lit. Philos. Soc.*, **41**: 14, (1887).[1] Schmiede-Knecht, *Genera Insect.*, **75**: 27, (1908). [1] India.

insidiator (Smith), n. comb.

Cryptus insidiator Smith, *Scient. Res. Sec. Yarkand, Miss.*, p. 21, (1878). ♀.[1] Schmiede-Knecht, *Genera Insect.*, **75**: 27, (1908). [1] Asia: Kashmir.

luculentus (Cameron), n. comb.

Cryptus luculentus Cameron, *The Entomologist*, p. 85, (1905). ♀.[1] Schmiede-Knecht, *Genera Insect.*, fas. **75**: 28, (1908). [1] India: Simla.

luteus (Cameron), n. comb.

Cryptus (= *Steriphocryptus*) *luteus* Cameron, *The Entomologist*, p. 234, (1903). ♀.[1] Schmiede-Knecht, *Genera Insect.*, fas. **75**: 28, (1908). [1] India: Darjeeling.

obscurus (Gravenhorst), n. comb.

Cryptus obscurus Gravenhorst, *Ichn. Eur.*, **2**: 548, (1829). ♀, ♂, excluding var. 2. Stephen, *Ill. M.*, **7**: 287, Ratzeburg, *Ichn. d. Forst.*, **1**: 141. Fonscolombe, *Ann. Soc. Fr.*, p. 376, (1850). Holmgren, *Sv. Ak. Handle.*, p. 51, (1854). Taschenberg, *Zeits. Ges. Nat.*, p. 86, (1865). Tschek, *Verh. z-b. Ges.*, p. 114, (1870). ♂, ♀. Thomson, *Opusc. ent.*, **5**: 481 (Part), excl. ♂. Dalla Torre, *Cat. Hymen.*, **3**: 582, (1901–02). Morley, *Ichn. Brit.*, **2**: 310, (1906). Schmiede-Knecht, *Genera Insect.*, fas. **75**: 29, (1908). Dutt, *Mem. Dep. Agric. India, Ent.*, **8** (2): 22, (1923).[1] [1] Punjab: Murree.

Var. *C. dianæ* Gravenhorst, *Ichn. Eur.*, **2**: 545, ♂. *et* var. 3. Morley, *Ichn. Brit.*, **2**: 310, (1906).

? var. *C. difficilis* Tschek, *Verh. z-b. Ges.*, p. 117, (1807). excl. ♀. Morley, *Ichn. Brit.*, **2**: 310, (1906).

Cryptus orientalis Cameron, *Mem. Proc. Manchester, Lit. Philos. Soc.*, **41**: 16, (1896–97).

rufopetiolatus (Cameron), n. comb.

Cryptus rufopetiolatus Cameron, *Trans. ent. Soc. Lond.*, p. 105, (1904). ♀.[1] Schmiede-Knecht, *Genera Insect.*, fas. **75**: 30, (1908). [1] Asia: Assam.

tricolor (Brulle), n. comb.

Cryptus tricolor Brulle, *Hist. Nat. Insect., Hymen.*, **4**: 195, (1846). ♂. Dalla Torre, *Cat. Hymen.*, **3**: 593, (1901–02). Schmiede-Knecht, *Genera Insect.*, **75**: 32, (1908).

IDIOLISPA Forster

Idiolispa Forster, *Verh. Naturh. Ver. Preuss, Rheinl.*, **25**: 188, (1868), (Type of genus: *Bassus analis* Gravenhorst). Morley, *Ichn. Brit.*, **2**: 296, (1906). Schmiede-Knecht, *Genera Insect.*, **75**: 34, (1908). Dutt, *Mem. Dep. Agri. India, Ent.*, **8** (2): 22, (1923). Townes, *Mem. Amer. ent. Soc.*, **11** (1): 251, (1944). Musebeck, Krombein, Townes and others, *U.S. Dep. Agric. Monograph*, **2**: 266, (1951).

Liocryptus Thomson, *Opusc. ent.*, fas. **5**: 471, 489, (1873). Schmiede-Knecht, *Genera Insect.*, fas. **75**: 34, (1908). Townes, *Mem. Amer. ent. Soc.*, **11** (1): 251, (1944), Synonyms of *Trychosis* Forster. Muesebeck, Krombein, Townes and others, *U.S. Dep. Agric. Monograph*, **2**: 266, (1951).

analis (Gravenhorst)

Basses analis Gravenhorst, *Vergl. übers, Zool. System.*, 266, (1807). Muesebeck, Krombein, Townes and others, *U.S. Dep. Agric. Monograph*, **2**: 266, (1951).

Cryptus analis Gravenhorst, *Ichn. Eur.*, **2**: 560, (1829). Excl. ♂. Ste., *Ill. M.*, **7**: 289. Tasch., *Zeit. Ges. Nat.*, p. 91, (1865). Tschek, *Verh.*

z-b. Ges., 126, (1870). ♂, ♀. Morley, *Ichn. Brit.*, **2**: 296, (1906).

Liocryptus analis Thomson, *Opusc. ent.*, **5**: 490; **21**: 2356, ♂, ♀. *Cf.* Brisch., *Schr. Nat. Ges. Danz.*, p. 333, (1879). Morley, *Ichn. Brit.*, **2**: 296, (1906).

? Var. *C. nubeculatus*, Var. 2 Gravenhorst, *Ichn. Eur.*, **2**: 490; **2**: 611, ♀. Morley, *Ichn. Brit.*, **2**: 296, (1906).

Ichneumon monotenus Ratz., *Ichn. d. Forstins.*, **1**: 155; **2**: 133, ♂. Morley, *Ichn. Brit.*, **2**: 296, (1906).

Idiolispa (= *Bassus a.*) *analis* Gravenhorst, *Vergl. übers. Zool. Syst.*, p. 266, (1807). SchmiedeKnecht, *Genera Insect.*, fas. **75**: 35, (1908). Dutt, *Mem. Dep. Agric. India, Ent.*, **8** (2): 22, (1923).[1] Muesebeck, Kromein, Townes and others, *U.S. Dep. Agric. Monograph*, **2**: 266, (1951).

[1]Assam: Khasia Hills.

DAGATHIA Cameron

Dagathia Cameron, *Mem. and Proc. Manchester, Lit. Philos. Soc.*, **47**: 29, (1903), (Type of genus: *Dagathia brunnea* Cameron). Schmiede-Knecht, *Genera Insect.*, fas. **75**: 43, (1908).

brunnea Cameron

Dagathia brunnea Cameron, *Mem. and Proc. Manchester Lit. Philos. Soc.*, **47**: 29, (1903). ♀.[1] Schmiede-Knecht, *Genera Insect.*, fas. **75**: 43, (1908).

[1] Assam: Khasia Hills.

AGLAOCRYPTUS Cameron

Aglaocryptus Cameron, *Mem. and Proc. Manchester Lit. Philos. Soc.*, **47**: 31, (1903), (Type of genus: *A. curvimaculatus* Cam.). Schmiede-Knecht, *Genera Insect.*, fas. **75**: 43, (1908).

curvimaculatus Cameron

Aglaocryptus curvimaculatus Cameron, *Mem. and Proc. Manchester Lit. Philos. Soc.*, **47**: 31, (1903). ♀.[1] SchmiedeKnecht, *Genera Insect.*, fas. **75**: 43, (1908).

[1] Asia: Khasia Hills.

striatifrons Cameron

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DAYRO Cameron

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pilosus Cameron

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NEMATOPODIUS Gravenhorst

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longiventris Cameron

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[1] Asia: Khasia Hills.

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EMBRYOLOGY OF TWO EUPHORBIACEÆ

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Introduction

The present communication deals with the embryology of *Euphorbia dracunculoides* Lamk. and *Euphorbia microphylla* Heyne. The former has been studied in greater detail while in the latter only the pollen grains and post-fertilization stages have been described since microsporogenesis and female gametophyte in this species are already studied by Jain.* No previous work is summarized here as it has recently been reviewed by Johri and Kapil (1953) and Kajale (1954).

Microsporogenesis and Male Gametophyte

The anthers are di-thecous. The archesporium, comprising two or three rows of hypodermal cells, cuts off a parietal layer. The latter by its divisions forms three layers. Consequently the anther wall including the epidermis consists of four layers (Figs. 1, 2). The epidermis persists till the end. The hypodermis as usual forms the fibrous endothecium (Fig. 4) in the mature anther. A few cells of this layer become progressively smaller towards the line of dehiscence on its either side while the epidermal cells over the corresponding area undergo a reverse change becoming enlarged in the radial direction (Fig. 3). These changes constitute the mechanism of dehiscence in the anther. Similar changes have been noted by the author in *E. hypericifolia* also (Mukherjee, 1957). Prior to dehiscence the cellular partition between the two pollen sacs disappear and they become confluent. The layer of cells inner to the endothecium degenerate during early stages of development (Fig. 3) while the innermost parietal layer forms tapetum of the secretory type. Its cells are uni-nucleate to begin with, but later they increase in size and become bi-nucleate when the pollen mother cells are undergoing meiosis. The tapetal cells degenerate *in situ* before the pollen grains reach maturity. Numerous small yellow staining granules appear

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first on the inner tangential walls of the tapetum and later on the endothecial cells (Fig. 4).

The pollen mother cells divide once mitotically. Each one of them later on enlarges and develops a mucilaginous sheath round it during prophase of meiosis I. The first meiotic division is immediately followed by the second, at the close of which cytokinesis begins and is effected by the formation of furrows (Fig. 5). The young pollen grains are arranged either in a tetrahedral or isobilateral manner (Fig. 6).

The young pollen grains are rich in cytoplasm and soon they develop exine and intine. As development proceeds they become enlarged and vacuolated. The nucleus is pushed to the periphery and remains embedded there is a thin layer of cytoplasm. Here it divides to form a generative cell and a tube cell. The former is situated in between the two furrows (Figs. 7, 9). The generative cell later divides to form two male gametes and the pollen grains are shed in this three-celled condition (Fig. 8) as in many other Euphorbiaceæ (*see* Johri and Kapil, 1953). The grains are spheroidal. They are tricolporate in *E. microphylla* (Fig. 10) and tricolpate in *E. dracunculoides*. Their equatorial diameter is 18–20 μ in the former and 30–40 μ in the latter species.

The exine is sharply differentiated into sexine and nexine. The former is baculate. The latter is conspicuously developed in the form of two inwardly projecting ridges oriented parallel to the direction of the polar axis. This change in the structure of the nexine occurs earlier in *E. microphylla* than in *E. dracunculoides* (Figs. 7, 9). The ridges of the nexine become fully developed only in the mature pollen grains just prior to shedding (Fig. 8).

According to Erdtman (1952) the thickness of the nexine varies in the Euphorbiaceæ. Generally it is thinner than the sexine but in some species like *Micrantheum ericoides*, *Neoscortechinia arborea* and *Stachystemon vermicularis* the condition is just the reverse and the nexine is thicker than the sexine. The thickness of the nexine inside the pollen grain in some species of the family is also not uniform. For instance, in *Hevea brasiliensis* var. *janerirensis* (Erdtman, 1952) the nexine is thicker at the operculæ than at other places. In the species under investigation on the other hand it becomes thicker in between the adjoining colpi in the form of two ridges as described above. The intine is a delicate membrane.

MEGASPOROGENESIS AND FEMALE GAMETOPHYTE

The gynoecium is tricarpellary and trilocular. Each loculus contains a single ovule hanging down from the apex of the axile placentation (Figs.

11, 12). The ovule is anatropous, bitegmic and crassinucellate. In *E. dracunculoides* the micropyle is formed by both the integuments. The nucellus is free from the inner integument up to the base and the nucellar beak does not protrude beyond the base of the endostome as in *Ricinus communis* (Singh, 1954), *Putranjiva roxburghii* and *Trewia nudiflora* (Banerjee and Dutt, 1949). In *E. microphylla* on the other hand the nucellar beak is well developed. It extends beyond the exostome and meets the obturator developing from the placenta (Fig. 11). The beak which tapers towards the apex consists of 4 or 5 cells at the tip. Towards the base, however, it is thicker.

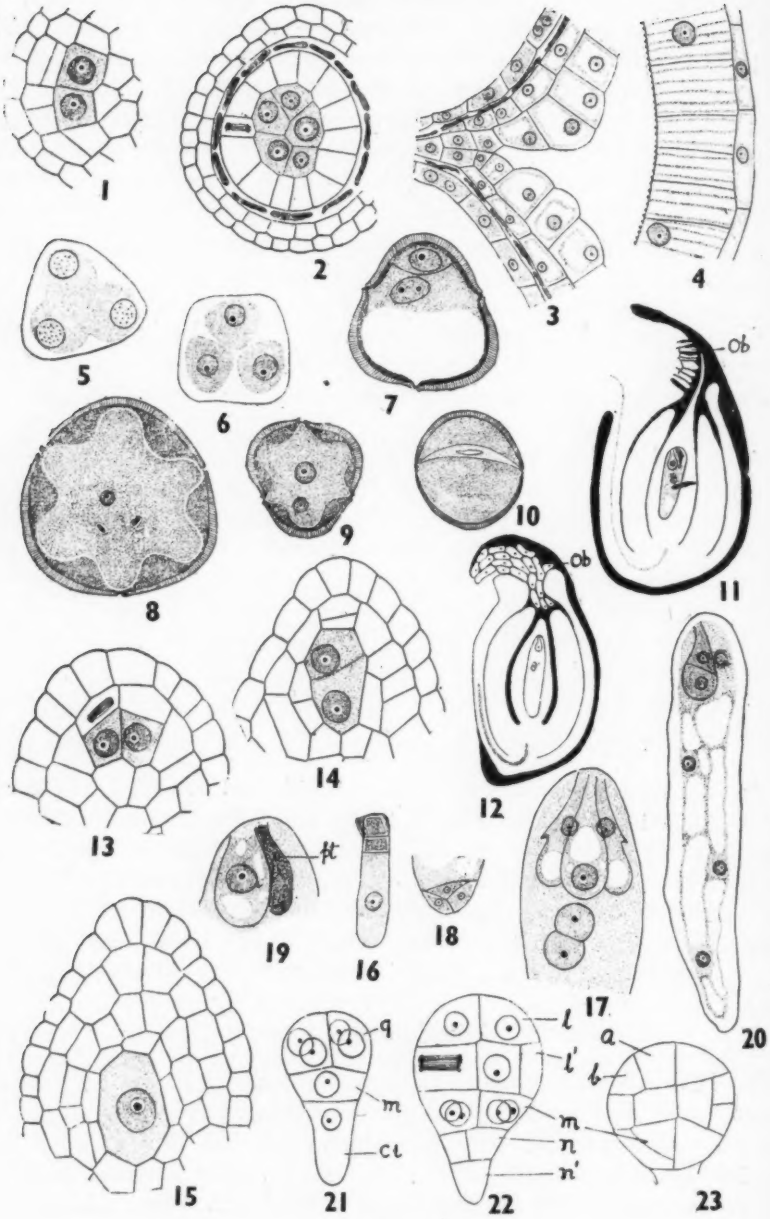
The obturator develops from the placenta. Unlike in several other species of the genus the obturator in *E. dracunculoides* enters the micropyle and meets the nucellar beak enclosed inside the endostome (Fig. 12).

The hypodermal archesporium is formed from two or three cells (Fig. 13). In a few cases it occupies a sub-hypodermal position also (Fig. 14). The archesporium cuts off parietal cells forming two or three megaspore mother cells (Fig. 13). However, only one develops further (Fig. 15) while the remaining merge into the nucellar tissue. The megaspore mother cell, after the two meiotic divisions, forms a tetrad either of a linear or T-shaped type (Fig. 16). The chalazal megaspore functions while the remaining three at the micropylar end degenerate. The nucleus of the functioning megaspore undergoes divisions forming an eight-nucleate embryo-sac of the Polygonum type (Maheshwari, 1950).

The egg apparatus consists of two synergids and one egg. The synergids are hooked and have long beak. They have a basal vacuole and their nucleus is in the micropylar part (Fig. 17). The egg is flask-shaped with a nucleus in the basal half and a vacuole in the micropylar portion. The two polar nuclei fuse below the egg apparatus and show increase in size prior to their forming a secondary nucleus (Fig. 17). This was observed only in *E. dracunculoides*. The antipodals are three short-lived cells (Fig. 18).

Fertilization

Fertilization is porogamous. The pollen tube during its passage through the embryo-sac destroys generally both the synergids (Fig. 19). It travels up to the base of the egg where it discharges its contents (Fig. 19). The antipodals are not traceable during fertilization. The fertilized embryo-sac, therefore, shows only the zygote and a single endosperm nucleus.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FIGS. 1–23

Endosperm

The primary endosperm nucleus in both the species divides once or twice forming 2 or 4 free nuclei (Fig. 20) before the egg divides transversely. The free nuclear division in the endosperm continues for sometime forming several nuclei which become placed in a thin layer of cytoplasm at the periphery. During further development each nucleus becomes enclosed by a cell-wall and the free nuclear endosperm becomes cellular. Part of it is utilized by the growing embryo but a sufficient amount of it persists in the mature seed surrounding the embryo. The seeds thus are endospermic, a feature characteristic of the entire genus. The endosperm is not uniformly distributed all round the embryo. More of it is present on the lateral sides than at the two ends. When the amount of endosperm at the two ends is compared it is seen that more of it is present over the tip of the cotyledons than over the radicle.

Embryo

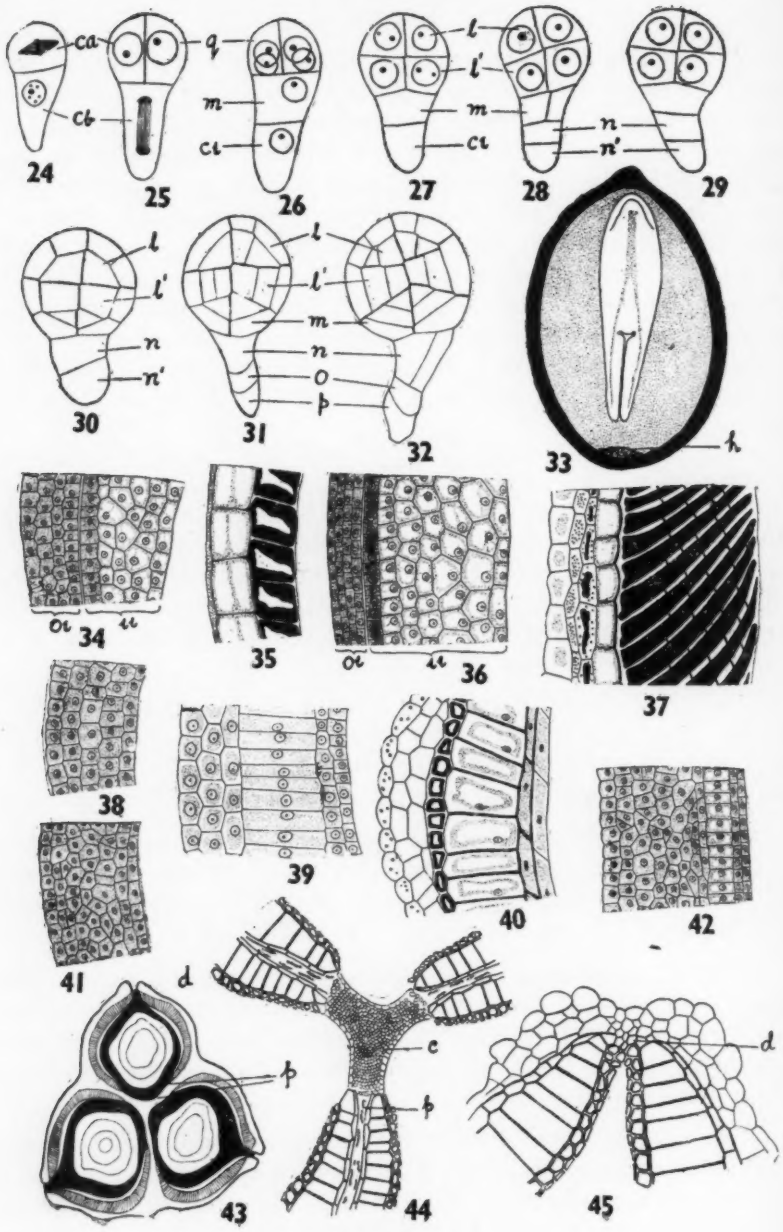
The first division of the fertilized egg is transverse (Fig. 20) unlike in *E. rothiana* (Shrivastava, 1952) and *E. preslii* (Weniger, 1917) where it is stated to be longitudinal. The two cells formed after the first division are designated as *ca* and *cb*. The next division occurs in the cell *ca* and is in the vertical direction forming a T-shaped pro-embryo consisting of three cells disposed in two tiers (Figs. 24, 25).

The cell *cb* divides transversely forming the cells *m* and *ci* (Figs. 21, 25, 26). The latter divides further into *n* and *n'* (Figs. 22, 28, 29). The cell *n'* by a transverse division forms *o* and *p* (Figs. 31, 32). Thus all the cells *m*, *n*, *o* and *p* are derived from the cell *cb* of the two-celled pro-embryo.

The two cells formed after the vertical division of *ca* divide again vertically forming four cells designated as *q* (Figs. 21, 26). Later each cell divides transversely resulting in an octant of two tiers, *l* and *l'* of four cells each (Figs. 22, 27, 29).

After the octant stage the two species follow a slightly different course of development. In *E. dracunculoides* the cells of the tier *l* divide obliquely (Fig. 23) cutting off four outer cells (*a*) and four inner cells (*b*). The former by its differentiation forms the two cotyledons of the mature embryo while the latter develops into the stem tip.

The penultimate tier *l'* consists of four cells. Its cells divide periclinally to cut off the dermatogen (Figs. 22, 23) before the formation of the cells *a* and *b* in the tier *l*. Later on the dermatogen appears in the other two tiers *m* and *l* also. But it is usually differentiated earlier in the tier *m* than in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FIGS. 24–35

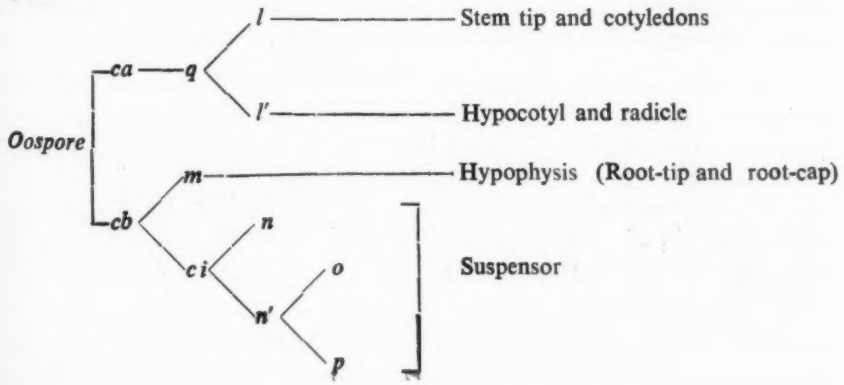
the tier *l* (Fig. 23). In the beginning the cells of the tier *l'* divide mostly in the vertical direction. But later on they divide both in the vertical and transverse planes ultimately developing into the hypocotyl and the radicle.

Development of the embryo in *E. microphylla* up to the octant stage follows the same course as in *E. dracunculoides*. But later on it differs slightly from the latter in that the tier *l* does not divide obliquely to form four outer cells (*a*) and four inner cells (*b*) as in *E. dracunculoides* (Fig. 30). Consequently the primordia of the cotyledons and the stem tip are differentiated a little later in the tier *l* in *E. microphylla* than in *E. dracunculoides*. Except for this difference the development of the embryo in the two species is similar.

The tier *m* begins as a single cell. While the octant is being organized it divides by two vertical walls at right angles to each other (Figs. 22, 28) forming four circumaxial cells. These divide further in a periclinal manner (Figs. 23, 30, 31). The four cells, cut off on the peripheral side, complete the dermatogen of the root-tip while the four inner cells contribute towards the formation of root cortex. The cells of the dermatogen during subsequent development divide both in the periclinal and anticlinal directions to organize the root-cap. The four inner cells divide once again periclinally (Fig. 32). The resulting outer cells form the periblem while the inner ones form the plerome.

The cells of the remaining tiers *n*, *o* and *p* develop into the suspensor which towards the embryo side (Figs. 22, 32) becomes multiseriate as in *E. hirta* (Kajale, 1934). The structure of the suspensor after the embryo becomes cordate is not studied.

The scheme given below summarizes the origin, disposition and differentiation of the different parts of the embryo from the oospore in both the species.



It is clear from the preceding description that the embryo development in both the species agrees in essential features with that of *E. exigua* (Souèges, 1925), *E. hirta* (Kajale, 1954) and *E. hypericifolia* (Mukherjee, 1957) conforming to the Euphorbia variation of the Onagrad type of Johansen (1950). According to the system of Souèges (*see* Johansen, 1950) it falls under period I and series A belonging to the Megarchetype IV.

MATURE EMBRYO

The mature embryo is straight and dicotyledonous. It is surrounded by the endosperm (Fig. 33). The three histogenic layers become clearly distinguishable. The periblem as seen in a longitudinal section consists of eight to nine layers of cells in *E. dracunculoides* and five to six in *E. microphylla* while the plerome consists of five to six layers in the former and three to four in the latter species. The root-cap attains its maximum thickness over the extreme root-tip where it consists of eight to nine layers in *E. dracunculoides* and five to six layers in *E. microphylla*. The plumule is a dome-shaped structure and is not differentiated into leafy parts (Fig. 33). The embryo has well-developed vascular tissue which ramifies in the region of the cotyledons. Laticiferous elements are also observed in the mature embryo.

The cells in the different histogenic layers contain numerous starch grains. The length of the hypocotyl and radicle including the root-tip is 120 μ in *E. dracunculoides* and 50 μ in *E. microphylla* and that of the cotyledons in the two species is 90 and 30 μ respectively.

HYPOSTASE AND SEEDCOAT

In the two species studied, a saucer-shaped pad of tissue becomes differentiated below the chalazal end of the embryo-sac as in *E. hirta* (Kajale, 1954) and functions as an hypostase. It persists in the mature seed as an organ of storage as its cells are full of starch grains.

The ovule has two integuments. The outer one consists of four cells throughout its length (Figs. 34, 36) but in *E. dracunculoides* its thickness increases up to twelve to fourteen layers in the region of micropyle. The inner integument, however, is thicker than the outer for the major part and consists of five to six layers of cells in *E. microphylla* (Fig. 34) and seven to eight layers in *E. dracunculoides* (Fig. 36). Towards the micropyle its thickness in both the species decreases by a few layers as in *E. hirta* (Kajale, 1954).

Both the integuments take part in the formation of the testa. The mature testa comprises three layers in *E. microphylla* and two or three layers

in *E. dracunculoides*. Its innermost layer becomes highly sclerosed forming a characteristic brittle stony layer known to occur in several other members of the family (Netolitzky, 1926; Landes, 1946; Johri and Kapil, 1953; Kajale, 1945; Singh, 1954 and Singh, 1959). This is derived from the outer epidermis of the inner integument in both the species while the other layers of this integument become crushed during development. The macrosclerides of the stony layer in *E. dracunculoides* are falcate and are obliquely oriented with their ends tapering on the endosperm side as in *E. geniculata* (Singh, 1959). Numerous pit canals are present on all sides of these sclerosed cells except on the outer tangential walls (Fig. 37). No such changes are noticed in the stony layer of *E. microphylla* where sclerosed cells become slightly elongated in the radial direction (Fig. 35).

Except the stony layer described above the remaining layers of the testa are derived from the outer integument. In *E. microphylla* there are two such layers representing both the outer and inner epidermis of the outer integument. The cells of the outer epidermis become flattened. They show in them the presence of numerous granules which look dark yellow in slides stained with hæmatoxylin (Fig. 35). The cells of the inner epidermis become enlarged and are without any contents. The mature testa thus consists of three layers in this species (Fig. 35).

In *E. dracunculoides* all the four layers of the outer integument persist for a long time along with the stony layer (Figs. 36, 37). The cells of the outer three layers also show granular deposits in them during later stages but ultimately they disappear. Sometimes, however, one of the layers persists in the mature testa. The cells of the fourth layer, which represents the inner epidermis of the outer integument adjoining the stony layer, do not show any such deposits but their inner tangential and radial walls become thickened and form one of the layers in the seedcoat. Thus in all, two or sometimes three layers derived from both the integuments contribute towards formation of the testa in this species.

Pericarp

The structure of the pericarp is studied in greater detail in *E. microphylla* than in *E. dracunculoides* where only a few stages have been described. The fruit wall in the former consists of five layers to begin with (Fig. 38) while in the latter it consists of seven to nine layers of parenchymatous cells (Fig. 41). As growth proceeds, the inner epidermis divides periclinally forming two layers (Figs. 39, 42) both of which become tangentially elongated and sclerosed in the mature pericarp (Fig. 40). The cells of the inner hypodermis become considerably elongated in the radial direction at right

angles to the two elongated layers formed by the inner epidermis. These hypodermal cells also become thick-walled. The cells of the layer immediately on its outer side in *E. microphylla* become sclerosed and elongated in a direction at right angles to the hypodermal layer (Fig. 40). In *E. dracunculoides* there are two such sclerose layers. The remaining outer layers continue to be parenchymatous. The cells of the outer epidermis show in them the presence of small granular deposits in *E. microphylla* (Fig. 40). No such deposits are, however, seen in the epidermal cells of *E. dracunculoides.*

The three sets of sclerotic layers described above are not formed on that part of the dorsal and placental side of the carpel marked *d* and *p* in Fig. 43. In these parts and also in the central portion of the septa marked as *c*, the cells remain parenchymatous and begin to degenerate as the fruit reaches maturity (Figs. 44, 45). The degeneration of these cells aided by the development of the three sets of sclerotic layers help in the dehiscence of the fruit (Figs. 44, 45).

SUMMARY

The paper deals with the life-history of *E. dracunculoides* with some observations on the development and structure of the pollen grains, endosperm, embryo, testa and pericarp of *E. microphylla.*

The archesporium in the anther is multicellular. The anther wall comprises the epidermis, fibrous endothecium, ephemeral middle layer and secretory tapetum. The tapetal cells become bi-nucleate prior to degeneration.

Cytokinesis is by furrowing. The young pollen grains are arranged either in a tetrahedral or isobilateral manner. They are spheroidal and tricolporate in *E. microphylla* and tricolpate in *E. dracunculoides.* The exine is differentiated into sexine and nexine. The latter is developed in the form of six prominent inwardly projecting ridges, two being located in between the adjoining colpi. The intine is a delicate membrane. Pollen grains are 3-celled at anthesis.

The gynoecium is tricarpellary and trilocular. Each loculus has one pendant, bitegmic, crassinucellate, anatropous ovule with upwardly directed micropyle. The placentation is axile. The nucellus forms a nucellar beak which in *E. microphylla* projects beyond the micropyle. In *E. dracunculoides* it reaches only up to the base of the endostome.

The female archesporium is hypodermal and multicellular. Subhypodermal archesporial cells are observed in *E. dracunculoides.* A parietal

cell is cut off. The tetrad of megaspores is usually of a linear type. The embryo-sac development conforms to the Polygonum type. Polar nuclei in *E. dracunculoides* increase in size prior to fusion. The structure of the egg apparatus is normal. The antipodals are represented by three ephemeral cells.

Fertilization is porogamous. The pollen tube destroys both the synergids during its passage through the embryo-sac.

The nuclear endosperm becomes cellular later. The seeds are endospermic.

The embryo development in both the species conforms to the Euphorbia variation of the Onagrad type or belongs to Period I series A Megarchetype IV. However, the embryo development in *E. microphylla* differs from that of the other species in that the formation of the dermatogen precedes the differentiation of the cotyledon and plumule initials in the tier *l* while in *E. dracunculoides* the formation of the dermatogen is delayed and the initials of the cotyledons and plumule are laid down before the dermatogen appears in the tier *l*.

The mature testa consists of two or three layers in *E. dracunculoides* and of three layers in *E. microphylla*. The innermost layer is stony and brittle. It is derived from the outer epidermis of the inner integument. The remaining layers of the mature testa in both the species are derived from the outer integument.

The structure of pericarp and its mode of dehiscence is described.

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EXPLANATION OF TEXT-FIGURES

FIGS. 1–8; 12–23. *Euphorbia dracunculoides*. Figs. 1, 2. Stages in the development of anther, × 600. Fig. 3. Part of anther wall before dehiscence showing bi-nucleate tapetum, degenerating middle layer, hypodermis and epidermis with some of its cells enlarged, × 600. Fig. 4. The same as above showing fibrous endothecium, × 600. Figs. 5, 6. Stages in cytokinesis, × 830. Figs. 7, 8. Bi-nucleate and 3-celled pollen grain; note the ridges of nexine in Fig. 8, × 500. Fig. 12. V.S. of ovule with obturator entering the micropyle; note that the nucellus is free up to the base, × 120. Fig. 13. L.S. of the nucellus showing 2 megaspore mother cells and 2 parietal cells, × 600. Fig. 14. Same as above showing sub-hypodermal archesporium, × 600. Fig. 15. Same as above showing functioning megaspore mother cell, × 600. Fig. 16. T-shaped tetrad, × 600. Fig. 17. Micropylar part of the embryo-sac showing egg apparatus and two polar nuclei, × 1,800. Fig. 18. Chalazal part of the embryo-sac showing 3 antipodals, × 600. Fig. 19. Micropylar part of the embryo-sac showing egg and pollen tube (*pt.*), × 600. Fig. 20. Embryo-sac in L.S. with 2-celled pro-embryo and free endosperm nuclei, × 235. Figs. 21–23. Stages in development of embryo, × 600. Figs. 9–11. *Euphorbia microphylla*. Fig. 9. 2-celled pollen grain showing ridges of the intine, × 830. Fig. 10. The same in surface view showing one of the colpi with a pore, × 830. Fig. 11. V.S. of ovule at mature embryo-sac stage, × 150. *ob*, Obturator.

FIGS. 24–32; 34, 35; 38–40; 43–45. *Euphorbia microphylla*. Figs. 24–32. Stages in the development of embryo, × 600. Figs. 34, 35. Stages in development of testa, × 600.

Figs. 38–40. Stages in development of pericarp; note the presence of granules in the outer epidermal cells in Fig. 40, × 300. Fig. 43. T.S. of fruit, × 60. Figs. 44, 45. Part of fruit wall at the time of dehiscence, × 120. Fig. 33, 36, 37, 41, 42. *Euphorbia dracunculoides*. Fig. 33. L.S. of mature seed; note the presence of hypostase, × 10. Figs. 36, 37. Stages in development of testa, × 230 and 300 respectively. Figs. 41, 42. Stages in development of pericarp, × 300. *h*, hypostase, *ii*, inner integument; *oi*, outer integument; *d* and *p*, dorsal and placental side of carpel; *c*, central portion of septa.

STUDIES ON FISH METABOLISM

I. The Effect of Temperature on the Heart Rate

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Introduction

Temperature is probably the most potent factor controlling the metabolism of animals (Krogh, 1916). In many animals it has been demonstrated that within limits of lethality the rate of any biological process undergoes a variation in the same direction as that of the temperature. The poikilotherms which have little or no body temperature regulation are more influenced by temperature changes than homoiotherms. They have their metabolic activities directly controlled by the temperature of the external medium. In fishes, for instance, a rise in temperature leads to an increased maintenance requirement and consequently almost all life processes such as feeding (Qasim, 1957), breeding (Hoar, 1957), development (Needham, 1942; Lindsey, 1954), growth (Brown, 1946), respiration (Fry and Hart, 1948) and so on, become temperature dependent.

The cardiovascular system of fish is no exception to this rule. Like other activities, almost all aspects related to this system also undergo significant changes by the variations in temperature. Earlier observations related to this system are generally available on those species which can withstand laboratory conditions and these include eels, dog fishes, skates and a few other forms (Mott, 1957). Studies related to the effect of temperature on the heart rate are very few and most of them have been undertaken in recent years. Dohrn and Rein (1950) pointed out a simple relationship between the frequency of heart beat in the dog fish *Scyllium stellare*, and the temperature of water which was being taken into the gills for respiration. Grodzinski (1950) observed an acceleration of heart rate in the trout embryo with the rise of temperature. Later on a similar effect was noticed in the isolated heart of eel, *Anguilla anguilla* (L.) (Grodzinski, 1954).

As noted above, the information available on the subject is mainly confined to a few species. The following studies were, therefore, under-

taken to establish the reaction of heart of several freshwater fishes to changes in temperature.

Methods

Fishes were made unconscious by inserting a sharp needle through the back of the cranium which injured the brain. They were then transferred into deep rectangular glass dishes containing Ringer's physiological saline (McClung Jones, 1950). To view the heart a triangular slit was cut open on the ventral side just above the heart. While making this operation particular care was taken to avoid bleeding as far as possible and in doing so the major blood vessels were left uninjured.

Temperature changes in the glass dishes were made by gradually adding warm or cold saline as required and in this way the fishes were subjected to a gradual rise and fall in temperature. Before making any observations on the heart rate, an interval of fifteen minutes was given so as to counteract any acceleration such as may arise in the heart as a result of pithing. A higher temperature, generally 30° C., was taken as the starting point of the experiment. It was decreased gradually and as soon as a desired level recording the difference of 5° C. was reached, the heart beat at that temperature was counted per minute. Thus the temperature was brought down to 5° C. in gradual steps and then again increased gradually upto 30° C. Before counting the heart rate at any temperature, an interval of five minutes was given so that the heart may attain a uniform pace. In small fishes the count of the heart beat was made with the help of a binocular microscope.

Nature of Heart Beat during Experiments

The heart of unconscious fishes continues to beat in the saline for 6–7 hours, the myogenic contraction starting from the sinus venosus and travelling through the auricle to the ventricle. During the first hour or so, the heart contracts vigorously and there is no significant change in the frequency of heart beat, but as the time advances, the contraction wave becomes weak and the heart rate gradually slows down. Towards the end, the beat of the ventricle becomes feeble and finally stops, but the auricle and the sinus venosus continue to beat over a much prolonged period.

There was a marked individual variation in the heart rate of the same species. Individuals of the same size and sex showed differences in the numbers of beats per minute. To counteract this difficulty, in the present investigation generally ten individuals or more were taken for each set of readings and the data related to the heart rate refer to the beat of the ventricle only.

TEMPERATURE RESPONSES OF THE HEART RATE

The heart rates of the following species were studied by giving them a routine of gradually decreasing and then increasing changes in temperature:

1. *Ophicephalus punctatus* Bloch.
2. *Mystus vittatus* (Bloch).
3. *Barbus stigma* (C. & V.).

Ophicephalus punctatus.—Three different size groups, namely the adult (18–19 cm.), the juveniles (5·5–6·5 cm.) and the young fishes (2·5–3 cm.) were taken to establish the relationship between the temperature changes and their heart rates. The data pertaining to these three groups are given in Fig. 1. The A part of the figure indicates the various frequencies of the heart at decreasing and increasing changes in temperature and the B part shows the averaged values of two different frequencies obtained at identical temperatures of 10°, 15°, 20°, 25°, and 30° C.

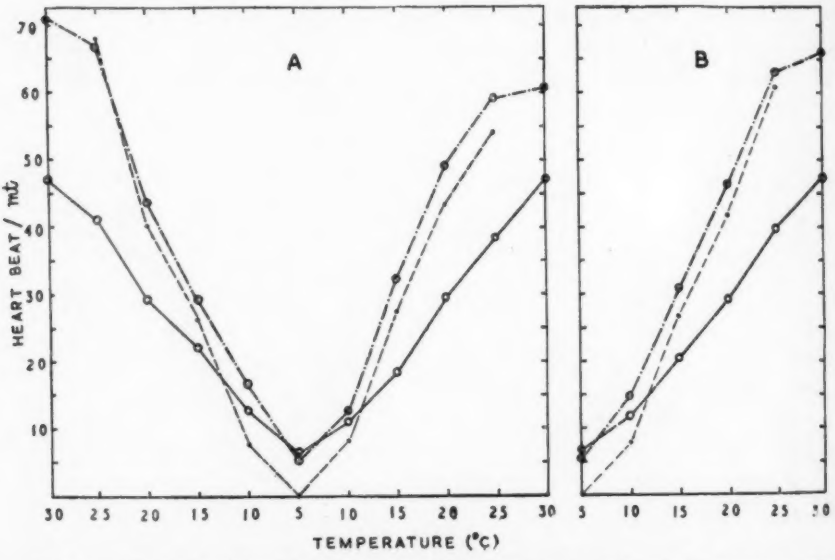

FIG. 1. Frequency of heart beat of *Ophicephalus punctatus* in relation to temperature. The A part of the figure shows decreasing and increasing changes in temperature and the B part shows the averaged values of two frequencies at 5, 10, 15, 20, 25 and 30° C.
O—— Adults; ⊙—·—Juveniles; ●— — — Young fishes.

As can be seen from the figure, in all the size groups the response of the heart rate was consistent and fell in accordance with the temperature

changes. The gradual decrease in temperature was followed by a steady fall in the frequency of heart beat and its subsequent increase after reaching the minimum value of 5° C. was accompanied with a gradual rise. The recovery of heart, however, was relatively slow and at the highest temperatures of 25° and 30° C. the earlier frequencies were never attained.

It can also be noted from the figure that at higher temperatures larger fishes have heart rates slower than the smaller ones. At 30° C. the heart of the adult fishes has a mean frequency of 47 beats per minute. Temperatures higher than 30° C. result in an immediate fall of the heart rate and at 35° C. which proves to be the upper lethal limit for the adult fishes, the heart begins to beat irregularly and eventually stops. In young fishes even 30° C. proves to be lethal. For these fishes the starting point of the experiment was taken as 25° C. At this temperature the heart maintains a uniform pace and registers a fall when the temperature is decreased. The lower lethal limit for the adults and juveniles lies below 5° C. In young fishes, on the other hand, the heart stops beating at 5° C. and continues to remain quiet for a few minutes until the temperature is again increased. At 10° C. it revives fully and begins to beat vigorously. With a further increase in temperature its frequency increases and reaches almost its maximum again at 25° C.

Mystus vittatus.—Observations were made only on fully grown individuals of this species measuring 12–13·5 cm. in length. Figure 2 gives the frequencies of the heart beat at various temperatures. It is clear from the

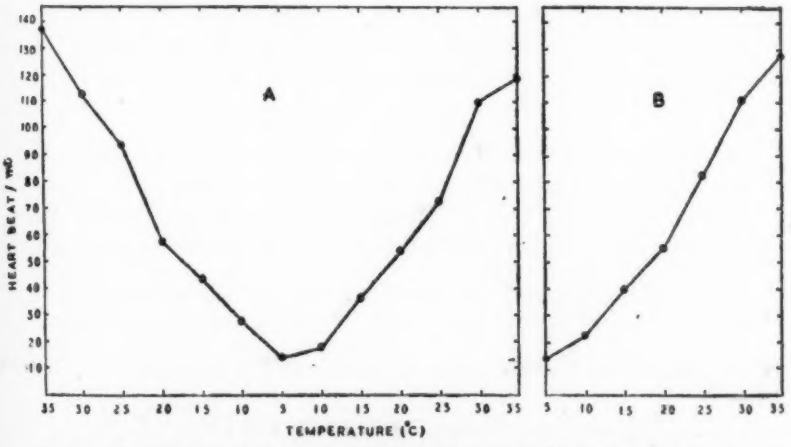

FIG. 2. Frequency of heart beat of *Mystus vittatus* in relation to temperature. Otherwise as in Fig. 1. Only adult fishes were used in experiments.

figure that the pattern of response in *Mystus vittatus* is very similar to that shown by *Ophicephalus punctatus*. There are, however, some important differences which can be summarised as follows:

As compared to *Ophicephalus punctatus*, the heart of *Mystus vittatus* has a much faster rate. It can also stand a wider range of temperature. At 35° C. which is lethal to *Ophicephalus punctatus*, it maintains its normal rhythm and at 30° C., it has a frequency 2·3 times greater than that of *Ophicephalus punctatus* at the same temperature. Further reduction in temperature brings about a fall in the heart rate but it is interesting to note that even at the lowest temperature of 5° C., the same difference in frequency, *i.e.*, 2·3 times greater than that of *O. punctatus*, is maintained.

Barbus stigma.—In this species also, experiments were made only on adult specimens measuring 9–10 cm. in length. The response of the heart at various temperatures is shown in Fig. 3. Unlike the other two species noted above, the heart of this species was most susceptible to changes in temperature. A gradual reduction in temperature was accompanied with a sharp fall in the heart rate and at 5° C., the heart becomes remarkably slow recording hardly more than 1–2 beats per minute. An increase from 5° C. was followed by a slow recovery which could never keep pace with the temperature beyond 25° C.

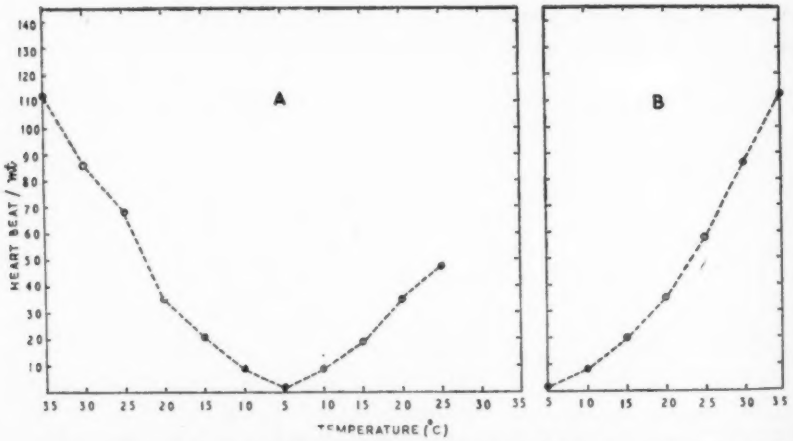

FIG. 3. Frequency of heart beat of *Barbus stigma* in relation to temperature. Otherwise as in Fig. 2.

TEMPERATURE CHARACTERISTICS OF THE HEART RATE

In studying the effect of temperature on biological processes, Q_{10} has often been used as a measure to determine the temperature effect. It is

also known as the 'temperature coefficient' or the ratio of velocity constants at temperatures having a difference of 10° C. The formula which has been widely used is as follows:

$$Q_{10} = \left(\frac{K_1}{K_2}\right)^{10/t_1 - t_2}$$

where K_1 and K_2 are velocity constants of biological processes corresponding to temperatures t_1 and t_2.

It has commonly been held that as in a chemical reaction where Q_{10} lies generally between 2 and 3 (Vant Hoff's rule), in most of the biological processes also the Q_{10} remains close to these values (Kanitz, 1915). This, however, is not always true as there have been some notable exceptions (Heilbrunn, 1945), but the fact that Q_{10} can be applied in many biological processes provides some basic similarities between a chemical reaction and a biological process.

If the heart-beat frequency in fishes is taken as a biological process, the Q_{10} in adult *O. punctatus* for 5–30° C. is 2·195. For the same range of temperature, the juveniles of this species have a higher Q_{10}, 2·696. In the young *O. punctatus* the heart stops beating at 5° C. If this temperature is excluded and the Q_{10} is calculated for 10–25° C. it is 3·931—a figure still higher than the previous two.

By taking Q_{10} values between 2 and 3 as indices of a biological process, a higher Q_{10} probably suggests a greater susceptibility to temperature changes. Certainly the three size groups of *Ophiocephalus punctatus* give a clear indication of this characteristic. The young fishes which have a higher Q_{10} are more susceptible to temperature changes than the juveniles and the adults.

It must also be noted that the same feature is reflected from the Q_{10} values of *M. vittatus* and *Barbus stigma*. The former species, which can withstand a wide range of temperature (5–35° C.), has a Q_{10}, 2·088. The later species which is less tolerant has a Q_{10}, 2·811 for 10–35° C.

Another temperature coefficient which has widely been used to study the temperature characteristics is the Arrhenius μ. This is derived from the well-known equation

$$K_1 = K_2 . e^{\mu/2(1/T_1 - 1/T_2)}$$

Here K_1 and K_2 are velocity constants at absolute temperatures T_1 and T_2.

Generally in all chemical reactions, the Arrhenius μ remains constant, but when applied to biological processes or enzymatic reactions, like Q_{10}, it shows distinct variations (von Euler, 1925).

The Arrhenius formula suggests the following linear relations:

$$y_1 = a - \frac{b}{T_1}\ ;\quad y_2 = a - \frac{b}{T_2}$$

where y_1 and y_2 are equal to log K_1 and K_2 at absolute temperatures T_1 and T_2 and a and b are constants. From the equation

$$y = a - \frac{b}{T}$$

it follows that if y (log K) is plotted against the reciprocal of absolute temperature (1/T), the points lie in a straight line suggesting that μ is a constant. In such cases the slope of the curve gives a measure of μ.

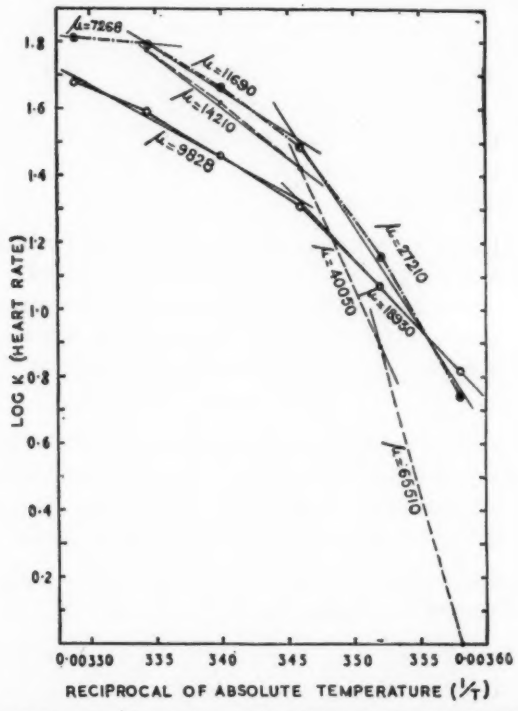

FIG. 4. *Ophicephalus punctatus.* The relationship between the logarithm of heart rate and the reciprocal of absolute temperature. μ-values corresponding to each straight line are also given.

○—— Adults; ⊙—·— Juveniles; ●— — — Young fishes.

Figs. 4 and 5 give the plotting of the data related to heart rates of various species under investigation. In these figures y is the log heart rate and $1/T$ is the reciprocal of absolute temperature. It can be seen from the figures that the points do not lie in a straight line. The curves in all the species under investigation have, therefore, been broken into a series of straight lines as suggested by Crozier and Stier (1925). This clearly represents that a certain temperature range has an independent action on the heart rate.

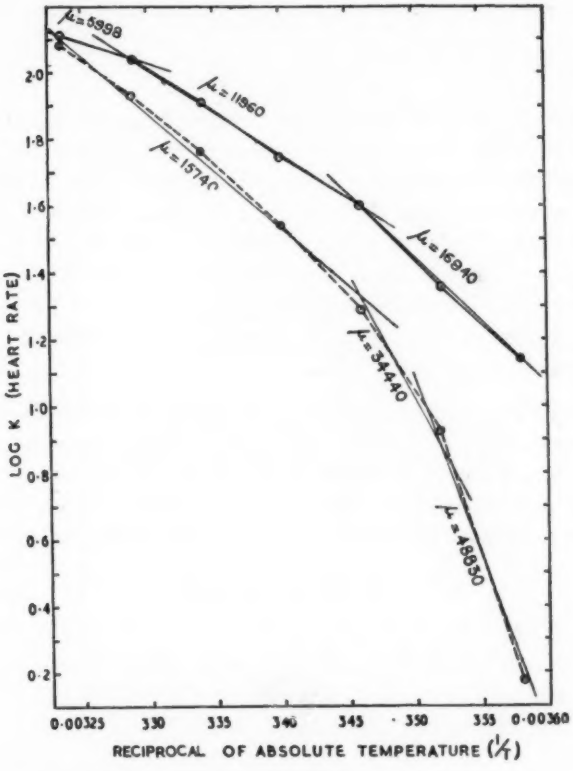

FIG. 5. The relationship between the logarithm of heart rate and the reciprocal of absolute temperature in other fishes. Otherwise as in Fig. 4.
⊙—— *Mystus vittatus*; ⊙— — — *Barbus stigma*.

It must also be noted that like other biological processes of poikilothermal animals, the temperature characteristics of heart rate follow the same general principle. At lower temperatures, the heart rate is very nearly inhibited, the Q_{10} and μ values are therefore usually much higher. Similarly

at temperatures above the optimum there is again a decrease in the vital activity as the thermal death point is approached. Here the Q_{10} and μ values are very low. These facts clearly explain the temperature characteristics presented in Figs. 4 and 5. Each straight line in the figures indicates that there is a single controlling reaction within a definite range of temperature. The μ values corresponding to each straight line, as calculated from the Arrhenius equation have been given in the figures. As can be noted from these values, in all the species investigated the μ values are low at a higher temperature range. At low temperature ranges they are relatively much higher.

SUMMARY

Three species of freshwater fishes, namely *O. punctatus*, *M. vittatus* and *B. stigma*, were taken to establish the effect of temperature on the frequency of heart beat. In *O. punctatus*, experiments were made on three different size groups to illustrate the differences in the heart rate between older and younger individuals. The response of heart in all the species is very similar. The decrease in temperature is accompanied with a fall in the frequency of heart beat and its subsequent increase is followed by a steady rise. Younger individuals show greater susceptibility to temperature changes than the juveniles and the adults.

The temperature characteristics of the heart rate have also been studied by using temperature coefficients Q_{10} and μ. Both these coefficients have been found to vary and it is suggested that the heart rate like other biological processes of poikilothermous animals is dependent on an optimum range of temperature as both high and low lead to an inhibition of vital activity.

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ROOT APICAL ORGANIZATION IN MONOCOTYLEDONS—ZINGIBERACEÆ

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Introduction

In some previous communications the authors have described the organization of the root apices of some members of Musaceæ and Cannaceæ of the order Scitamineæ (Pillai and Pillai, 1961 *a*, *b*, *c*) and of *Sorghum vulgare* Pers. (Pillai and Sachdeva, 1960). It has been sufficiently emphasized in them that the anatomical study of the structural configuration alone is not sufficient to give a complete picture of the organization of the root apices and that the cyto-physiological aspects should also be studied for this purpose. In this communication the organization of the root apices of ten members belonging to seven genera of the family Zingiberaceæ of Scitamineæ is described.

Materials and Methods

The methods for the study of the members of Musaceæ described already (Pillai and Pillai, 1961 *a*), *viz.*, fixing the materials in CRAF (or refixing them if they were fixed on the spot in F.A.A.), washing them four to five times—each time for 15 to 20 minutes—in 70% alcohol (Johansen,1940), dehydrating and clearing in xylol and imbedding in paraffin of various melting points according to the season of the year, were followed here also. Sections were cut at 7 to 10 μ thickness. Safranin and fast green, Iron-alum hæmatoxylin and Pyronin and methyl green staining schedules were followed.

The root apices of the following species were investigated: *Curcuma longa* Linn., *C. aromatica* Salisb., *Costus speciosus* Sm., *Alpinia calcarata* Rosc., *Elettaria cardamomum* Salisb., *Hedychium coronarium* Koen., *Kæmpferia galanga* Linn., *K. rotunda* Linn., *Zingiber zerumbet* Rosc. and *Z. officinale* Rosc.

Observations

There are two types of structural organization met with among these species, one type being exhibited by the first nine species, for which a common

description is given, and the other shown by *Zingiber officinale*, which is described separately.

TYPE 1. *With 3 sets of structural initials, one each for the root-cap and plerome, and a common zone for dermatogen and periblem.*

Root-cap.—This has two distinct regions, the columella in the middle and a peripheral region around it, distinguishable by the different types of cell complexes.

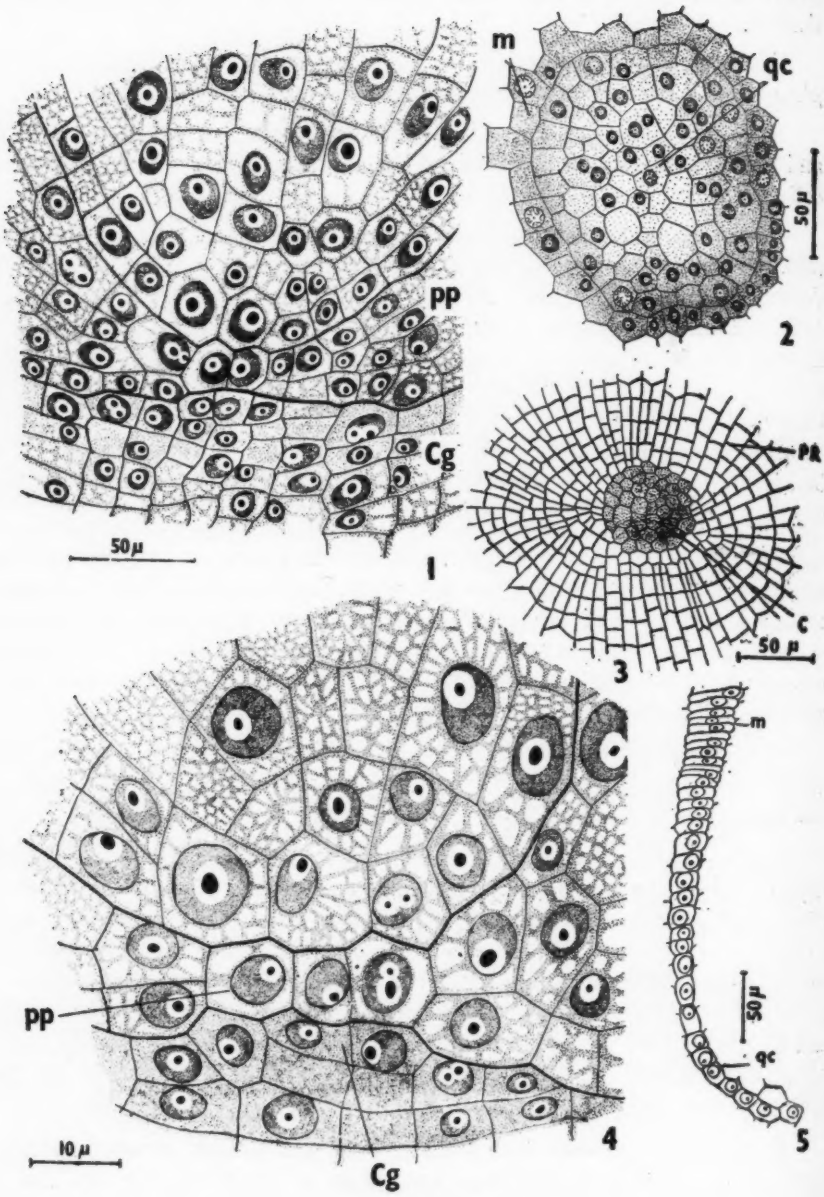
Columella.—This is composed of cells arranged in vertical superimposed files. It appears to arise by the activity of a meristem which can be easily differentiated (Schopf, 1943; Allen, 1947; Spurr, 1949; Pillai and Pillai, 1961 *b*) from that concerned with the formation of the rest of the cap and more or less fitting into a depression at the tip of the root body (Text-Figs. 4, 6, 8, 9, 11 and 13). The name the authors (Pillai and Pillai, 1961 *b*) had given to it, *viz.*, *columellogen*, is continued to be applied to it. It was also found by the authors while tracing its development in lateral roots that this meristem becomes distinct from that concerned with the formation of the rest of the cap very early in the development of the lateral root.

Peripheral region is distinguished from the columella by the different orientation of its cell-rows which are oblique files curving from the flanks toward the columella. Frequent T-type divisions occur with the capital of the T directed towards the flanks (*t* in Text-Figs. 8, 13, etc.) which enable this region to broaden out towards the front. The name *peripheral region*, given by Allen (1947), is adopted here also.

In transections, the cells of the columella form a compact mass of polygonal cells in the centre with the cells of the peripheral region arranged in radiating rows around it (Text-Fig. 3).

It appears that the columellogen does not contribute to the peripheral region because the column maintains long vertical files of cells, the number of cells across at different levels remaining the same. This shows that once a cell becomes established as part of the column, it does not contribute cells to or become transformed into a cell of the peripheral region. Spurr (1949), in the roots of *Pinus strobus* and Pillai and Pillai (1961 *b*) in *Canna indica* and *C. edulis*, have found similar arrangements, whereas Schopf (1943) and Allen (1947) have found that the more lateral cells of the column shift polarity and grow out obliquely to form the peripheral region.

Histogens of the root body.—As pointed out earlier, structurally two histogens could be distinguished: (1) the plerome concerned with the formation of the stele, and (2) the protoderm-periblem complex, concerned with



TEXT-FIGS. 1–5

the formation of the outer shell to the stele, including the periblem and dermatogen.

The *Protoderm-periblem complex* is located outside the plerome and is composed of a single tier of cells varying from 2 to 10 cells across in the various species (Text-Figs. 4, 6, 13, etc.). This tier is distinguished with some difficulty because of the state of quiescence of the cells at the tip of the root body.

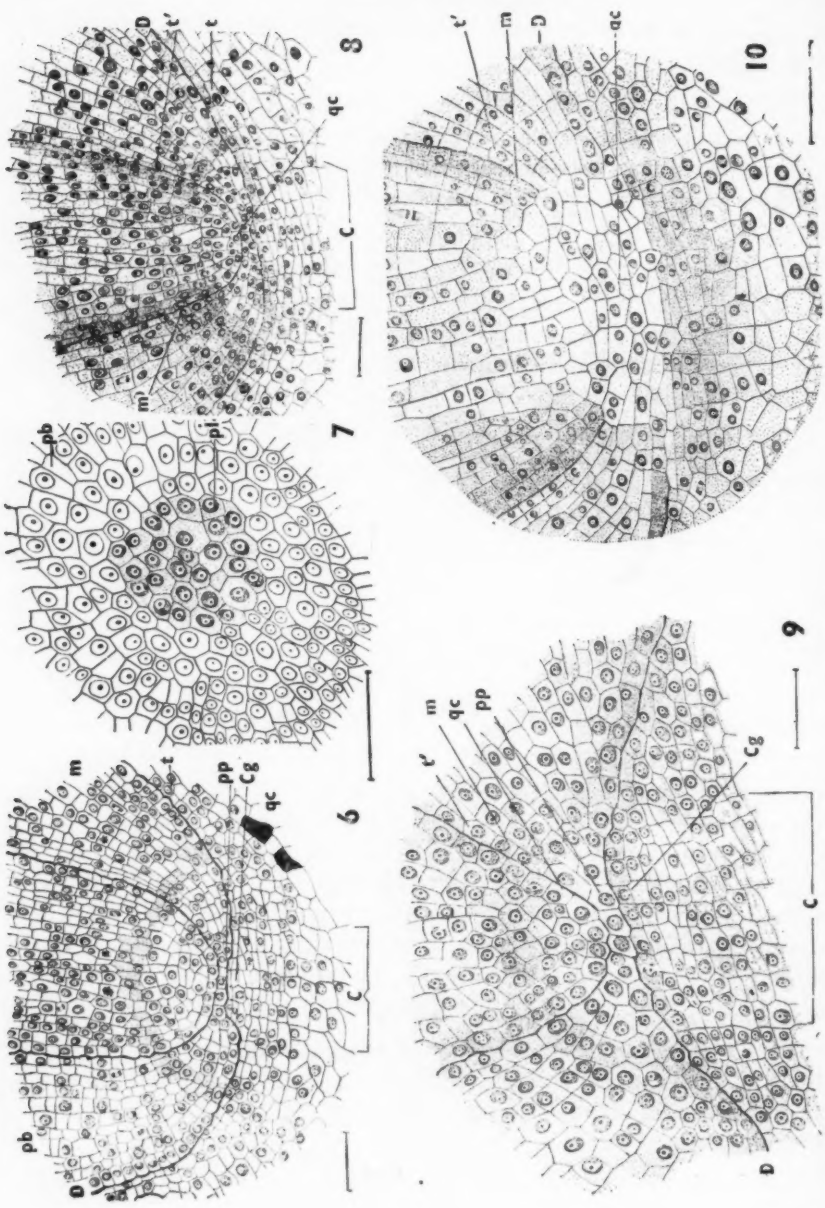
The cells of this zone located on the flanks exhibit T divisions with the T-head pointed towards the middle, *i.e.*, the *Körper* type of division (Schüepp, 1917). This enables the tissue to widen out. Repetition of such T divisions results in the formation of the concavity at the tip of the root body into which, as pointed out earlier, the columellogen fits.

Dermatogen.—This separates out as a distinct layer from the products of division of the protoderm-periblem complex at some distance on the flanks. This tier, from now on, divides only anticlinally and henceforth is concerned with the formation of the epidermis only (D in Text-Figs. 6, 8, 12, etc.). It is, therefore, in a narrow sense, as was used by the authors before (Pillai and Sachdeva, 1960; Pillai and Pillai, 1961 *a*, *b*), that this expression is used. In the quiescent centre these cells are comparatively elongated radially whereas in the meristematic zone behind it they are thin, radially flattened and due to repeated division, appear like a stack of coins (Text-Fig. 5). In other words, the cells are actively dividing in the latter region.

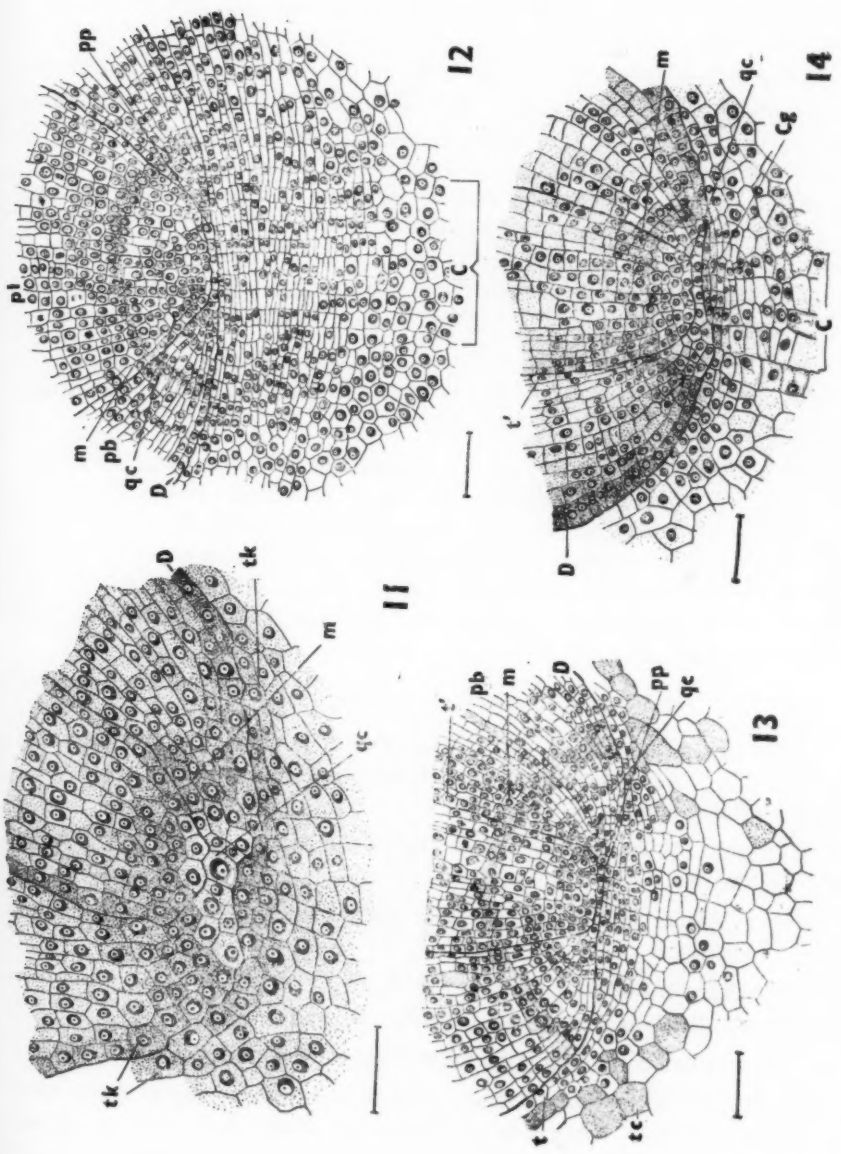
Periblem and its derivatives.—The term periblem is applied to the initials of the cortex extending from the hypodermis to the endodermis. An analysis of the cells on the inner and outer sides of the dermatogen shows that there are curving rows arranged in opposite directions. Towards the tip are the cells of the calyptra already described where the cells show T divisions from the sides towards the centre with the capital of the T on the flanks. The cell rows towards the inside are arranged in the opposite direction with the T-head towards the plerome dome (Text-Figs. 6, 12, 13, etc.). After the periblem is wide enough the cells divide mostly anticlinally like a rib meristem.

Hypodermis arises from the inner of the twin daughter cells of the T divisions of the protoderm-periblem initials. The cells composing this tissue vacuolate earlier than the other cells of the cortex and their walls are crumpled also.

Endodermis differentiates from the innermost periblem cells. Outside the plerome dome all cells of the periblem exhibit T divisions (t in Text-Figs. 8, 9, 13, etc.). Only after a few such divisions does the innermost layer stop



TEXT-FIGS. 6–10



TEXT-FIGS. 11–14

divisions of that type and instead, exhibit anticlinal divisions. It is only now that the endodermis is formed. So, the endodermis, as pointed out before (Pillai and Pillai; 1961 *b*), can be said to arise from an endodermis-periblem complex.

Plerome has at its tip a group of more or less isodiametric cells. On the sides of the plerome dome is the uniseriate pericycle. Near the dome these cells are not densely staining because of their state of quiescence, whereas they show dense cytoplasm to a long distance behind the root-tip. The metaxylem vessel elements with wider lumen can be seen near the plerome dome vacuolating earlier. The isodiametric cells at the very centre of the plerome divide like a rib meristem to give rise to the pith. In transections passing near the tip of the plerome dome, the plerome initials can be distinguished as a compact mass of isodiametric cells (Text-Fig. 7) surrounded by radiating rows of periblematic cells.

TYPE 2. *With a common group of initials from which all the various zones arise.*

This is exhibited by the root-tip of *Zingiber officinale* only. From the rim of this common group differentiate out in their respective positions the calyptrogen, dermatogen, periblem and plerome (Text-Fig. 10). The root-cap cannot be distinguished into the columella and peripheral region and as such there are no separate initials for these. In the other features like the activity of the dermatogen, periblem and plerome, this root resembles the others described above.

CYTO-PHYSIOLOGICAL ORGANIZATION

Notwithstanding the structural configurations described above, the root tip (excluding the root-cap) can be distinguished into two zones on cyto-physiological grounds.

The *quiescent centre* found at the tip of the root body, characterised by its cells having:

(1) cytoplasm lightly stained with pyronin-methyl green and hæmatoxylin,

(2) smaller nuclei and nucleoli (Table II),

(3) cell divisions less frequent (Table I), and

(4) vacuolation noticeable in most (Text-Figs. 1 and 4).

In median longisections this group of cells is in the shape of a cup with the brim forwards. The above characteristics show their state of repose because of which Clowes (1956 *a* and *b*) has named it the quiescent centre

TABLE I

Number of cells in the quiescent centre and meristematic zone, number of dividing cells and the percentage of division (as determined in one transection of each root)

Species	Quiescent centre			Meristematic zone		
	Total No. of cells	No. of dividing cells	Percentage of division	Total No. of cells	No. of dividing cells	Percentage of division
Alpinia calcarata ..	66	Nil	0·00	274	74	27·0
	52	3	5·77	84	26	31·0
	124	3	2·42	95	38	40·0
	95	4	4·21	158	30	19·0
	81	5	6·17	133	37	28·0
Kæmpferia galanga	43	10	23·25	156	110	70·5
	64	16	25·00	130	61	47·0
	63	16	25·40	153	80	52·6
	50	14	28·00	132	62	47·0
	50	17	34·00	167	76	46·0
Kæmpferia rotunda	50	4	8·00	126	37	29·3
	68	7	7·90	168	58	34·5
	50	4	8·00	153	50	32·6
	62	5	8·00	265	93	35·3
	66	8	12·00	177	59	33·3
Curcuma aromatica	114	8	7·00	302	95	31·4
	81	5	6·20	249	84	33·5
	108	10	9·20	288	90	31·2
	32	3	9·30	185	80	43·2
	78	5	6·40	180	76	42·2
Curcuma longa ..	58	3	5·10	50	26	52·0
	60	3	5·10	54	27	50·0
	24	Nil	0·00	28	14	50·0
	29	2	7·00	45	20	44·4
	63	2	3·10	117	18	11·0

TABLE I—(*Contd.*)

Species	Quiescent centre			Meristematic zone		
	Total No. of cells	No. of dividing cells	Percentage of division	Total No. of cells	No. of dividing cells	Percentage of division
Costus speciosus ..	20	2	10·00	51	22	43·1
	34	4	11·70	55	32	58·1
	34	3	9·00	149	46	31·0
	50	4	6·00	92	38	41·2
	43	2	4·60	95	12	12·6
Elettaria cardamomum	170	12	7·00	206	36	17·5
	133	8	6·00	145	27	11·7
	150	10	6·60	200	32	16·0
	150	9	6·00	145	28	12·0
	145	10	7·00	140	25	18·0
Hedychium coronarium	49	3	6·00	237	83	35·0
	53	5	9·60	167	60	39·5
	59	6	10·00	169	56	32·9
	88	4	4·50	234	66	28·2
	116	6	5·10	281	72	25·7
Zingiber zerumbet	32	Nil	Nil	44	27	61·4
	35	3	8·50	45	28	61·5
	47	4	8·50	67	36	53·8
	52	6	11·50	59	29	50·0
	32	2	4·20	90	26	29·0
Zingiber officinale ..	87	10	11·40	135	43	31·8
	85	6	7·00	120	36	30·0
	87	9	10·00	125	35	28·0
	80	4	5·00	140	45	32·1
	79	3	3·70	129	38	29·4

This zone embraces and includes cells belonging to all the structural histogens of the root body; in other words, it is not structurally delimitable. It gradually merges with the zone outside, the meristematic zone. Its size is also variable, being smaller in thin roots and larger and more pronounced in older and thicker roots (Table I).

The meristematic zone.—Shaped like an arch and surrounding the quiescent centre on the side of the root body in longisections, are cells:

(1) with cytoplasm more deeply stained with pyronin-methyl green and hæmatoxylin,

(2) showing divisions more frequently (Table I),

(3) showing larger nucleoli and nuclei (Table II), and

(4) where vacuolation is not so prominent.

This zone also includes the cells of all the structural histogens of the root body.

In transections passing through these zones in some of these roots, the total number of cells and the number of dividing cells (where the nuclei show any stage of mitosis) were counted (Table I) and the percentage of division is found to be much lower in the quiescent centre than in the meristematic zone. The respective areas of the cell, nucleus and nucleolus and the nucleus/cell and nucleolus/nucleus ratios were calculated from some of the cells of each of these zones (Table II). These ratios are found to be lesser in the cells of the quiescent centre. These and the responses to stains like pyronin-methyl green indicate that these cells are in a state of comparative repose and hence are not synthesizing nucleic acids. Caspersson and Schultz (1939), Brachet (1952) and Clowes (1956 *a* and *b*, 1959 *a*) have shown by other methods that there is reduced synthesis of nucleic acids in the cells in a quiescent state and *vice versa* in those cells which are actively dividing.

Another feature in support of the quiescence of these cells and that of the repeated division of those behind is shown by the cells of the dermatogen which appear long and broad at the former zone and short and narrow and arranged like a stack of coins in the latter (Text-Fig. 5). In transections the quiescent centre appears as a group of lightly stained cells surrounded by a ring of deeply stained ones of the latter zone.

Discussion

The structural configuration at the root apices of the first nine members described above falls under Type 2 of Janczewski (1874), Treub (1876), Haberlandt (1914), Hayward (1938), Popham (1952) and Esau (1953). These

TABLE II

Areas of cell, nucleus and nucleolus in the qniescent centre and meristematic zone in Sq. μ (mean of 20 determinations) and the respective nucleolus/nucleus and nucleus/cell ratios

Species	Quiescent centre					Meristematie zone				
	Cell	Nucleus	Nucleolus	Nucleolus / Nucleus %	Nucleus / cell %	Cell	Nucleus	Nucleolus	Nucleolus / Nucleus %	Nucleus / Cell %
Curcuma longa ..	73·91 ± 22·58	17·793 ± 2·711	1·2488 ± 0·3396	7·018	24·07	55·07 ± 20·14	21·643 ± 7·358	2·0165 ± 0·5131	9·316	39·29
Alpinia calcarata ..	43·59 ± 16·94	11·886 ± 2·757	1·0088 ± 0·2211	8·480	27·26	61·19 ± 22·62	16·826 ± 6·377	1·316 ± 0·4392	7·820	27·49
Zingiber zerumbet ..	103·69 ± 40·54	20·879 ± 5·846	1·463 ± 0·5146	7·010	20·13	69·96 ± 5·33	20·539 ± 7·957	2·0603 ± 1·6895	10·030	29·35
Kæmpferia galanga ..	95·23 ± 27·79	27·162 ± 10·721	0·2560 ± 0·0256	3·530	28·52	67·61 ± 19·42	26·118 ± 9·507	2·7875 ± 0·0943	6·340	38·62
Costus speciosus ..	90·92 ± 33·51	22·815 ± 6·859	1·1173 ± 0·3807	4·890	25·09	66·07 ± 33·77	17·208 ± 5·600	1·7488 ± 0·5531	10·160	26·04
Zingiber officinale ..	33·48 ± 10·81	10·577 ± 2·896	0·4934 ± 0·1507	4·66	31·59	41·41 ± 9·85	13·350 ± 6·153	1·2984 ± 0·4384	9·72	32·22
Kæmpferia rotunda ..	90·53 ± 25·94	23·180 ± 10·125	0·7865 ± 0·2277	3·39	25·60	96·42 ± 21·82	31·186 ± 4·231	2·6245 ± 0·3381	8·41	32·34
Curcuma aromatica ..	69·42 ± 28·13	15·046 ± 4·679	0·5861 ± 0·2015	3·89	21·67	59·08 ± 27·52	14·192 ± 4·178	1·2899 ± 0·3654	9·08	24·01
Hedychium coronarium ..	45·31 ± 16·68	11·223 ± 4·088	0·3881 ± 0·1235	3·45	24·77	85·34 ± 22·02	9·368 ± 2·698	0·7950 ± 0·2504	8·48	10·97

authors feel that this is a type mainly found in grass-root apices. But the present investigation, those on Cannaceæ reported earlier (Pillai and Pillai, 1961 *b*) and those on Marantaceæ and Xyridaceæ, to be described later, go to show that this is quite prevalent in other monocotyledons also. Popham (1952) mentions it as the principal monocotyledonous type although the examples he quotes are from among the Gramineæ members. Pillai and Sachdeva (1960) have found it in *Sorghum vulgare* and so it may be common enough among the grasses. The authors, however, feel that this is an important type of structural configuration among monocotyledons.

Root-cap formation.—As in members of Cannaceæ (Pillai and Pillai 1961 *b*) the root cap is independent. Hanstein (1868) and Haberlandt (1914) assume the calyptra to be a proliferation of the dermatogen and do not consider any separate histogen to be responsible for its formation. Holle (1876) considers the root-cap to arise in two ways in all plants; (1) where root-cap originates from an apical cell, and (2) where the root-cap arises from the periblem. Holle has not considered the possibility of an independent histogen in its formation.

The cap is, as in Cannaceæ members, distinguishable into the central columella and the peripheral region. Here also, independent histogens characterised by two different types of cell division could be distinguished. The columella is produced by one whose cells divide mainly transversely whereas the rest of the cap is produced by another meristem whose cells exhibit the T-type of division. The expression " peripheral region " used by Allen (1947) is used here also for the latter and the term " columellogen " which the authors introduced is continued to be applied to the former.

In *Zingiber officinale*, where the cap has no independent origin, it can be considered as a proliferation of the root body. It is not distinguishable into the columella and peripheral region.

Histogens of the Root Body

Protoderm-Periblem complex.—Clowes (1954) has termed this the Dermoperiblem while Kasapligil (1954) refers to it as the Protoderm-Periblem complex. According to Haberlandt (1914) dermatogen and protoderm are not synonymous. Protoderm refers to the outermost layer of the apical meristem which gives rise to the epidermis only or to the sub-epidermal layers also whereas the dermatogen has its own independent initials and gives rise to the epidermis only. Thus, protoderm is more comprehensive and so is preferred by the authors in the expression protoderm-periblem complex, as they did before (Pillai and Pillai, 1961 *b*). This, of course, does not refer to the root apex of *Zingiber officinale*.

Dermatogen.—Esau (1953) opines that in roots the " dermatogen is supposed to be the outermost layer of the cortex ". In these roots this layer does not arise from an independent tier of initials but separates out from the protoderm-periblem complex, which type has been referred to by Clowes (1950, 1953) as arising from the cortex complex. This does not, of course, apply to the roots of *Zingiber officinale*. As pointed out before (Pillai and Pillai, 1961 *b*) this term is used in a restricted sense, because, once distinct, its cells divide anticlinally and produce the epidermis only.

Endodermis.—Earlier authors have considered the origin of this tissue to be as variable as its phylogenetic development (Haberlandt, 1914, pp. 391–92) and that it has been considered as both the innermost layer of the cortex and the outermost layer of the stele (Eames and MacDaniels, 1947, p. 160). Pillai and Pillai (1961 *b*) have pointed out that this arises from a histogen like the uniseriate dermatogen which separates out from the cortex complex. Near the plerome dome, the innermost layer of periblem cells exhibit T divisions, from the products of which separate out the dermatogen towards the outside and the endodermis towards the inside. The interpretation of Williams (1947) and Bekel (1956) that the endodermis is also meristematic in the early stages does not seem to be quite correct and it seems more appropriate to designate it as arising from an endodermis-periblem complex.

Plerome.—Initials for this are independent and normal in their activities giving rise to the pericycle, vascular elements and pith.

In *Zingiber officinale* there is a common group of initials from around which separate the various structural zones. Unlike the roots of members of Musaceæ, where a " central group " could be recognized, here this is not found. Thus, neither the " central cell " theory of Guttenberg (1940) nor the " initial group " theory of Brumfield (1943) is applicable here. It seems more appropriate to apply the term " promeristem " as used by Clowes (1953, 1954) to the configuration met with here.

CYTO-PHYSIOLOGICAL ORGANIZATION

These roots also, irrespective of their structural configuration, exhibit a group of cells constituting a quiescent centre. This is surrounded by cells in a more active state. This region has been named by the authors (Pillai and Pillai, 1961 *a*, *b*) the *meristematic zone*. This region appears to be the actual site of histogenetic activity as shown by some surgical experiments (Pillai and Sachdeva, 1960 *d*; Pillai and Pillai, 1961 *c*). The similarity between these regions and the *meristeme d' attente* and the *anneau initial* postulated by Plantefol (1947) and Buvat (1952) has already been pointed out.

The distance between the tip of the root body and the nearest mature phloem element, which carries the metabolic products required by the active cells, was found to be 200 μ to 500 μ in these species (Table III). This further supports the suggestion (Pillai and Pillai, 1961 *a*, *b*) that the cells at the tip of the root body go into quiescence because of the dearth of sufficient metabolites. These studies further support the view put forward earlier (Pillai and Pillai, 1961 *a b*, *c*) that a study of the root apical organization will not be complete without a study of the cyto-physiological state of the cells comprising the root apex. Clowes (1959 *b*) has also recently emphasized this aspect.

TABLE III

Levels of origin of metaxylem, protoxylem and phloem and level of mature phloem from the tip of the root body (in μ)

Species	Level of origin of			Level of appearance of mature phloem
	Metaxylem	Protoxylem	Phloem	
Alpinia calcarata ..	50–55	90–95	80–85	350–360
Kæmpferia galanga ..	55–60	180–185	130–135	350–360
Kæmpferia rotunda ..	25–30	70–80	50–55	250–260
Curcuma aromatica ..	60–65	250–260	70–75	180–185
Curcuma longa ..	50–55	215–220	120–130	300–305
Costus speciosus ..	65–70	160–165	125–130	160–165
Hedychium coronarium	50–55	130–135	90–95	290–300
Zingiber zerumbet ..	70–75	120–125	100–105	280–285
Zingiber officinale ..	50–55	360–365	155–160	480–490

SUMMARY AND CONCLUSIONS

The root apices of ten species belonging to seven genera of the family Zingiberaceæ exhibit two types of structural configuration. Nine of them have independent initials for cap and plerome and a common protoderm-periblem complex, while the tenth has common initials for all the tissues.

Where the cap is separate, there could be distinguished two initiating zones. The columellogen in the middle which fits into a concavity at the

tip of the root body is characterised by cutting off cells only transversely to the front producing the columella. The other showing T divisions and concerned with the production of the rest of the cap is the peripheral region.

The origin of the endodermis is traced to an initiating zone common with the periblem, the endodermis-periblem complex.

The cyto-physiological state of the cells has great importance from the histogenetic point of view. Here also could be distinguished a quiescent centre to the root tip with the meristematic zone composed of actively dividing cells around and behind it. The characteristics of the cells composing these two zones are described. It is further emphasized that this aspect should also be studied in addition to the structural configuration to have a more complete picture of the apical organization.

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EXPLANATION OF TEXT-FIGURES

TEXT-FIGS. 1–5. Fig. 1. *Kæmpferia galanga*. L.S. of root-tip to show the cyto-physiological state of the cells, they being vacuolated in the root body and not so in the root cap. Fig. 2. *Zingiber officinale*. T.S. of root passing through the quiescent centre surrounded by the meristematic zone. Fig. 3. *Curcuma aromatica*. T.S. of root-cap showing columella composed of compactly arranged polygonal cells in the middle surrounded by radiating rows of cells of the peripheral region. Fig. 4. *Alpinia calcarata*. L.S. of root-tip magnified to bring out the cyto-physiological state of the cells. Note the vacuolation in the cells of the root body but not in those of the root-cap. Fig. 5. *Hedychium coronarium*. Portion of the root apex bringing out the dermatogen with rectangular cells in the quiescent centre and the thin, short and broad cells arranged like a stack of coins at the meristematic zone.

C—Columella; Cg—Columellogen; m—Meristematic zone; pp—Protoderm-periblem complex; PR—Peripheral region; qc—Quiescent centre.

TEXT-FIGS. 6–10. Fig. 6. *Kæmpferia rotunda*. Median L.S. of root apex showing independent plerome and root-cap, and protoderm-periblem complex. Fig. 7. *Curcuma longa* T.S. passing through plerome tip surrounded by radiating rows of periblem cells. Fig. 8. *Costus speciosus*. Median L.S. of root apex having discrete plerome and root-cap, and protoderm-periblem complex. Fig. 9. *Hedychium coronarium*. Median L.S. of root-tip showing independent plerome and root-cap, protoderm-periblem complex and the quiescent centre. Fig. 10. *Zingiber officinale*. Median L.S. of root apex showing the common group of initials from around which differentiate the plerome, periblem, dermatogen and calyptrogen. The cells of the quiescent centre surrounded by the meristematic zone can be seen.

C—Columella; Cg—Columellogen; D—Dermatogen; m—Meristematic zone; pb—Periblem; pl—Plerome; pp—Protoderm-periblem complex; qc—Quiescent centre; t—Divisions of the peripheral region of the cap; t'–Divisions of the endodermis-periblem complex. (All scales = 50 μ).

TEXT-FIGS. 11–14. Fig. 11. *Elettaria cardamomum*. Median L.S. of root-tip with independent plerome and root-cap, and protoderm-periblem complex. Fig. 12. *Alpinia calcarata*. Median L.S. of root apex showing independent initials for plerome and root-cap, and common protoderm-periblem complex. The stippled region shows the outer limit of the quiescent centre. Fig. 13. *Curcuma longa*. Median L.S. of root apex showing discrete plerome and root-cap, and protoderm-periblem complex. Fig. 14. *Zingiber zerumbet*. Median L.S. of root apex with discrete plerome and calyptra and protoderm-periblem complex, the quiescent centre and the meristematic zone.

C—Columella; Cg—Columellogen; D—Dermatogen; m—Meristematic zone; pb—Periblem; pp—Protoderm-periblem complex; qc—Quiescent centre; t—Divisions of the peripheral region of the cap; t'—Divisions of the endodermis-periblem complex; tc—Tanniferous cells; tk—Divisions of the *Körper* and *Kappe* complexes. (All scales = 50 μ.)

ON TERMINAL SCLEREIDS AND TRACHEOID IDIOBLASTS

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INTRODUCTION

As far back as 1885, Heinricher observed in several plants the occurrence of enlarged storage tracheids either in a free state or at the terminus of vein ends. Solereder (1908) enumerated 24 families of dicotyledons in which several taxa showed the presence of enlarged terminal tracheids. He emphasised the need for further work on this subject. Haberlandt (1914) reported the occurrence of such storage tracheids and regarded them as local reservoirs for storage of water. Comparable tracheoid idioblasts are reported in several seed plants (Pirwitz, 1931, Pass, 1940). Foster (1956) designated such cell forms 'Tracheoid idioblasts'; they resemble tracheids in their spiral thickenings or pitted walls and differ from them in shape, size and topography. Recent investigations (Foster, 1944; Rao, 1957 *a*) indicated the existence of diversified types of terminal cells at the ends of veins in a large or small vein islet. The present study was undertaken to assess the importance of such cells in comparative morphology.

MATERIAL AND METHODS

The materials were derived partly from fresh plants and partly from herbarium specimens. The writer is indebted to the Curators of Bogor Botanical Garden, Indonesia and New York Botanical Garden for the supply of fresh and herbarium specimens. Thanks are also due to the Director, Scientific Co-operation Office, UNESCO, New Delhi, for procuring herbarium specimens from the U.S.A. The technique of clearing the leaves is already outlined (Rao, 1957 *a*).

OBSERVATIONS

Olacaceæ.—The presence of sclereids is not common in this family. Edelhoff (1887) and Colozza (1904) recorded the presence of diffuse sclereids in several species of *Heisteria*, *Cathedra* and *Anacolosa*. Recently Foster (1947) reported terminal sclereid-like cells in the leaf of *Ptychopetalum*. Similar cell forms have been observed in certain species of *Olax* and *Heisteria*.

In *Olax scandens* Roxb., *O. wightiana* Wall., and *O. zeylanica* L., the cleared lamina shows the presence of sclereid-like cells at the vain endings (Fig. 1). The terminal cells have an irregular form. Most of them are oblong, triangular or spherical and occur in twos and threes distinctly at the vein ends. The slightly sclerosed cells have a broad lumen. The cell wall shows innumerable pits and is devoid of helical thickenings.

In agreement with the observations of Edelhoff (1887) and Colozza (1904) the present study has revealed the existence of short fusioid diffuse sclereids in the mesophyll tissue of *Heisteria brasiliensis* Engl., *H. cauliflora* Sm., and *H. flexuosa* Engl. However, the vein-ends in these taxa show the presence of irregularly shaped slightly thickened cells. They exhibit the same features as in the species of *Olax*. In *H. chippiana* Standl., *H. longipes* Standl., *H. nitida* Engl., and *H. scandens* Ducke the lamina is free from sclereids. However, all these species posses slightly thickened cells at the vein-ends. Such cell forms are irregular in shape, possess abundant pits and are devoid of helical thickenings.

Capparidaceæ.—Of the 58 species of *Capparis* examined, sclereids were found only in *C. amygdalina* Griseb., *C. angustifolia* H. B. & K., *C. cyanophallophora* L., *C. indica* (L.) F. & R., *C. jamaicensis* Jacq., *C. odoratissima* Jacq., *C. orbiculata* Wall., *C. rotundifolia* Rottl., *C. verrucosa* Jacq.

The sclereids of *C. amygdalina*, *C. angustifolia*, *C. cyanophallophora*, *C. indica* and *C. jamaicensis* are short and prop-like and show more or less uniform distribution in the lamina. Most of the sclereids are diffuse, vertically disposed and do not show a terminal relationship with the vein ends. Storage tracheids with helical thickenings occur at the vein-ends.

In *C. angustifolia* the sclereids are short cell forms and occupy the epidermal and palisade regions of the mesophyll. They are mostly pyriform to fusiform and have a short unbranched plug-like process disposed amidst the epidermal cells. The main bulged portion is situated in the palisade region and does not show any forking, but the lower end is sometimes forked. The sclereids have a thick straited wall. There is a broad

median lumen in the bulged portion and a narrow or occluded lumen in the rest of the cell. The leaf is xeromorphic. In *C. odoratissima*, the sclereids exhibit the same pattern of distribution as in *C. angustifolia* but they are short, fusiform or filiform having a plug-like process in the epidermal region and branched or unbranched ending at the other pole.

In *C. orbiculata*, *C. rotundifolia* and *C. verrucosa* variously branched polymorphic sclereids with terminal disposition are found (Rao, 1953). They are short, filiform, irregular, asymmetrical and possess short processes which give them the characteristic gnarled forms.

In *C. koi* Merr., *C. moonii* Wt., *C. pumila* Champ., *C. spinosa* L., var. *canescens* and *C. viminea* HK.f. & T., the vein ends possess tracheoid idioblasts and slightly sclerosed sclereid-like cells. They are oval or semi-circular or irregular in shape. The cells have a broad lumen without any spiral thickenings. In *C. angulata* R. & P., *C. callophylla* BL., *C. cerasifolia* DC., *C. micracantha* Dc., *C. salicifolia* Griseb., *C. spinosa* L., *C. subacuta* Miqu., *C. tweediana* Eichl., and *C. zeylanica* L., the vein-ends are free from 'Tracheoid idioblasts' and sclereids. However, sometimes small dilated cells are present at the vein-ends.

Vochysiaceæ.—Solereder (1908) reported the presence of much elongated, spirally thickened storage tracheids in the mesophyll of *Vochisia rufa* Mart., and branched sclerenchymatous cells and fibres in the leaf tissues of *Lightia licanoides* and *Trigoniastrum hypoleucum* respectively. The storage tracheids of *V. rufa* which are in connection with the tracheæ at the terminations of the veins, are tubular and often traverse the entire thickness of the leaf in a perpendicular direction. The vascular bundles of the larger and smaller veins in *Erisma violaceum*, *Vochisia rufa*, *Salvertia convallariaecodora* and *Trigonia lævis* are provided with a sclerenchymatous investment of variable strength, but this is absent in *Callisthene fasiculata* and *Trigonia volnensiana*.

Of the 12 species of *Vochisia*, sclereids were present in *V. elliptica* Mart., *V. furcanosum* Mart., *V. ahupensis* Spr., and *V. magnifica* Warm. They are terminal or subterminal and not abundant. The sclereids have slightly sclerosed cell wall and lumen of irregular width. The sclereids of *V. magnifica* are more or less spherical or sub-spherical. The lamina exhibits prominent terminal tracheids. Terminal tracheids have prominent spiral thickenings whereas terminal sclereids possess slightly sclerosed walls and pits in abundance. This situation is similar to *Memecylon leucocarpum* (Rao, 1957 *a*).

In *V. calophylla*, the veins and vein-lets are densely covered with sclerenchyma. Mostly they extend beyond the vein-end as in *Mimusops hexandra* (Rao, 1951) and *Uvaria macrophylla* (Rao, 1953). In *V. parviflora* Spr., the sclerenchyma accompanying the veins extends beyond the vein-ends.

In *V. tomentosa* Dc., and *V. parviflora* Spr., sclereids are absent but the vein-ends possess prominent tracheoid idioblast of varied shape and size. Sclereids and terminal tracheoid idioblasts are absent in the leaves of *V. cinnamomea* Pohl., *V. ferruginea* Mart., *V. hænkeana* Mart., and *V. laurifolia* Warm.

Goodeniaceæ.—The leaf anatomy of members of Goodeniaceæ is incompletely known (Solereder, 1908). The occurrence of peculiar tracheoid idioblasts in a few species of *Scaevola* prompted me to examine the range of distribution and variation in some of the available species of *Scaevola*.

Of the 18 species of *Scaevola* examined sclereids were encountered only in *S. anchusæfolia* Bth., *S. canescens* Bth., *S. glabra* H. & A., *S. glandulifera* Dc., *S. globulifera* Labill., *S. holosericea* De Vriese, *S. hookeri* F. Muell., *S. lanceolata* Benth., *S. longifolia* De Vriese, *S. lobelia* Murr., *S. sp.*, and *S. tripida* Cav. Cleared leaves show that sclereids are of diffuse type and appear either as idioblasts or in groups of twos and threes in the mesophyll. They are polymorphic and range from simple globular, or rectangular to forking gnarled cell forms. Mainly there are three form types:

Type I.—Spherosclereids. They are seen in *Scaevola* sp. and *S. holosericea*. Sclereids are spherical or subspherical with much branching in *Scaevola* sp. whereas in *S. holosericea* the spherical or subspherical sclereids exhibit a strong trend towards bigger size and some of them become rectangular with number of processes at the corners. The transection of *S. holosericea* reveals the uniform distribution of these curious sclereids especially on the adaxial side and they form prominent cells inside the lamina. Irrespective of their varied forms the cell wall is sclerosed and exhibits striations often dotted with pit canals. The lumen is irregular and devoid of crystals.

Type II.—Polymorphic, small rectangular cell forms. They are encountered in *S. anchusæfolia*, *S. canescens*, *S. glabra*, *S. glandulifera*, *S. globulifera*, *S. hookeri*, *S. lanceolata*, *S. longifolia* and *S. tripida*. The sclereids are small rectangular cell forms with striated thick sclerosed wall and possess irregular lumen. Inside the lamina they are present as isolated cells and very rarely in groups of threes and fives, but in no instance they were found to fuse together. It is not uncommon to observe 'sclerocysts' in *S. glabra*. The sclerocysts are composed of 3–5 cells closely juxtaposed and unlike

the sclerocysts of *Memecylon parviflorum* (Rao, 1957 *a*) they do not encircle the vascular bundles.

Type III.—Sclereid-like cell at the vein-ends. Such cell forms are seen only in *S. saligna* and *S. lobelia*. They are spherical or sub-spherical forms present at the vein-ends along with prominent tracheoid idioblasts (Figs. 2–5). The cell wall is slightly sclerosed and straited. Most of them are spirally thickened or sometimes they possess a wide lumen of irregular pitting. Similar cell forms are seen in *Capparis religiosa* and *Olax* sp.

In *S. dajoensis* Merr., *S. oppositifolia* Roxb. and *S. chamissoniana* Gaud., the vein-ends are free from sclereids and storage tracheids whereas in *S. crassifolia* storage tracheids of varied shape are present at the vein-ends. It is not uncommon to observe slightly sclerosed diffuse forms in the lamina of *S. hookeri* and *S. frutescens*.

Discussion

The present study shows the existence of different forms of terminal cells. In the majority of the investigated species, the terminal cells are either sclereids or tracheoid idioblasts. However, the existence of intermediary cells is reported in certain species of *Mouriria* (Foster, 1946), and *Memecylon* (Rao, 1957 *a*) and this investigation shows their presence in certain species of *Olax* and *Capparis*, *Scaevola* and *Vochisia*. It is now worthwhile to compare sclereids and tracheoid idioblasts. Between them there are certain common features. Sclereids are terminal, diffuse or of the mixed type. Similarly tracheoid idioblasts are situated at the vein-endings or as diffuse idioblasts (Solereder, 1908; Habarlandt, 1914; Pirwitz, 1931; Pass, 1940; Foster, 1956; Rao, 1953, 1957 *a*, 1957 *b*). Foster (1947) reported terminal sclereid-like cells in the leaf of *Ptychopetalum* (Olacaceæ). In pattern of distribution there is a good deal of similarity. In certain species of *Olax* (Rao, 1957) the terminal sclereid-like cell resemble certain tracheoid idioblasts which occur in *Capparis religiosa* (Pirwitz, 1931). Both exhibit a varied shape and size in the same leaf. Sclereids and tracheoid idioblasts also resemble in their ontogeny. Just as tracheoid idioblasts originate from adjacent cells of the ground meristem (Pirwitz, 1931) sclereid ontogeny has revealed a similar type of origin. However, the mature sclereids differ from the tracheoid idioblasts in one respect. Sclereids have slightly or heavily sclerosed cell wall with pits, whereas, as a rule, the tracheoid idioblasts are thin-walled with pitted secondary walls. Another distinguishing character is that while certain tracheoid idioblasts show the presence of spiral thickenings they are not present in sclereids.

The present study supports the view (Rao, 1953, 1957 *a*, 1957 *b*, 1958) that the genus which has well-developed terminal tracheoid idioblasts will have some species or all species with well-developed terminal sclereids. It is further seen that in a genus exhibiting tracheoid idioblasts and terminal sclereids sometimes it is not uncommon to observe in certain vein-ends the existence of intermediary cell forms. A clear example is seen in *Mouriria* (Foster, 1946), *Memecylon* (Rao, 1957 *a*), *Niebhuria* (Rao, 1958), and *Capparis*, *Scaevola* and *Vochisia* (Present study).

SUMMARY

Contrasted forms of terminal cells have been observed in certain taxa of *Olax*, *Capparis*, *Scaevola* and *Vochisia*. The exact morphology of intermediary cell forms could only be known by studying their ontogeny in detail. The resulting data would throw interesting information on the question of homology among various types of cells.

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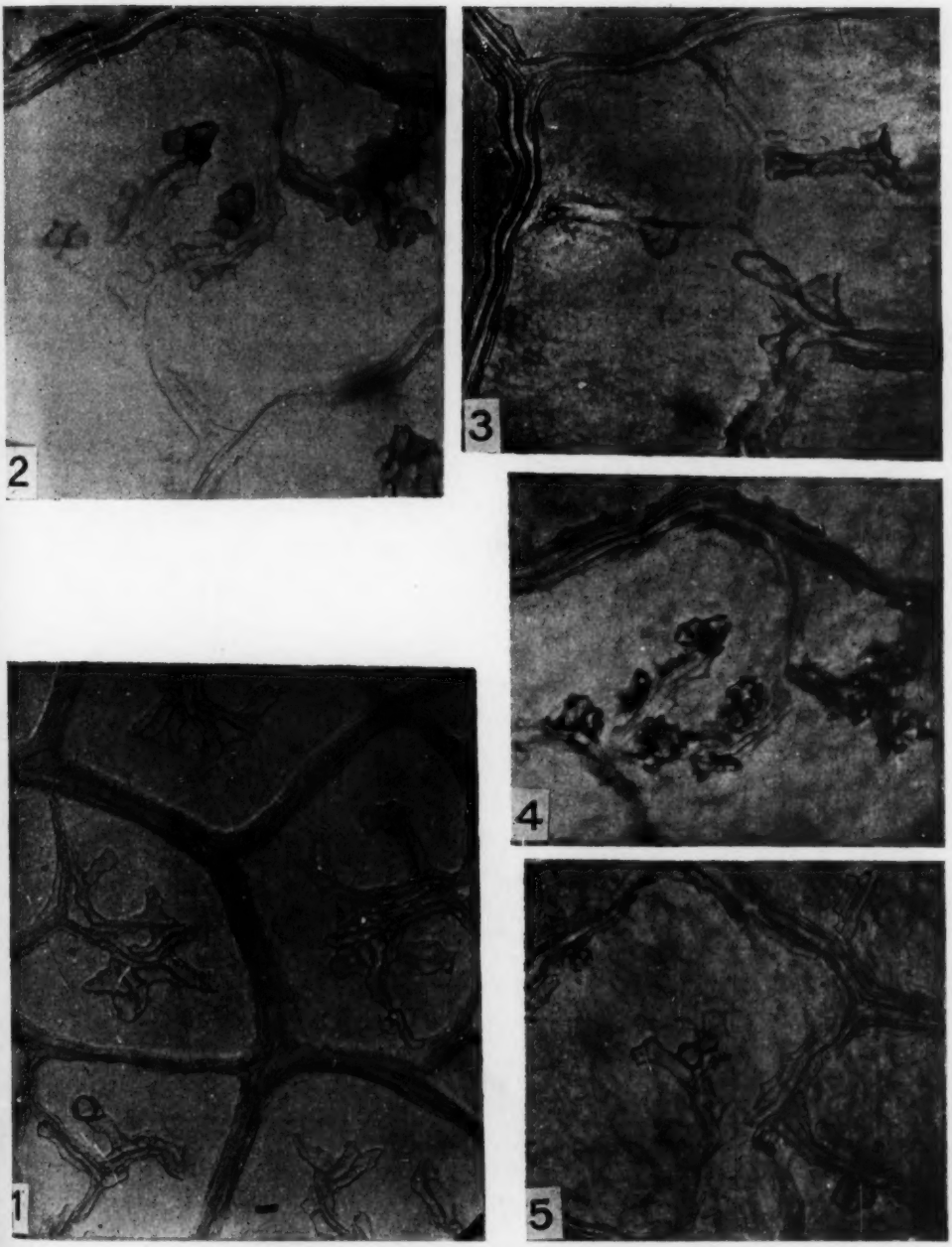

FIGS. 1–5. Cleared leaf portions showing diversified types of terminal cells.
FIG. 1. *Olax scandens*, × 200. Figs. 2–5. *Scævola lobelia*, × 200 each.

OBSERVATIONS ON THE EXTERNAL MORPHOLOGY OF *LIBURNIA FURCIFERA* (HORVATH) (HOMOPTERA, FULGOROIDEA, ARÆOPIDÆ)

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I. Introduction

Aræopids (Delphacidæ) are an interesting group of Fulgoroidea characterised by the presence of well-developed mobile spurs at the apex of their hind tibiæ. They bear a superficial resemblance to Jassids in general form, habits and habitat, but the former can be easily distinguished by the presence of tibial armature. There has been little study on the Araeopidæ in India. In regard to this group Lefroy (1909) had affirmed that no family would so well repay study from every point of view. Despite this statement there has not been much addition to our knowledge of this family, particularly on morphology, except for the cataloguing of a few of its forms by Distant

(1916) and Muir (1921, 1922). The present paper deals with the external morphology of *Liburnia furcifera*. According to Muir (1919), *Megamelus* (*Liburnia*) *furcifera* (Horvath) is identical with *Sogata pallescens* Distant, and *Sogata distincta* Distant, which have been recorded as pests of the paddy crop in various parts of India, such as Bihar, Bengal, Central Provinces, and Mysore, as well as in Ceylon and Malaya outside India. In 1915, a serious and widespread infestation in the Central Provinces was investigated by the Central Agricultural Research Institute, Pusa. The species in question, thus, appears to be of much economic importance. It was first described by Horvath (1899), and recorded for the first time from India by Distant (1906).

II. Material and Method

The insects were procured from electric domes, where they were found attracted to light. They were also caught by sweeping grasses near marshy places. They were preserved in a solution made up of formalin, acetic acid and alcohol. Head, wings and legs were separately mounted in balsam. The male genitalia were severed from specimens and put in cold concentrated potassium hydroxide solution for about five minutes at room temperature. They were then transferred to glacial acetic acid and kept for about five minutes. The material was then dissected out under stereoscopic binocular microscope according to the method described by Giffard (1921), after which it was dehydrated in carbol-xylol mixture and mounted in balsam.

III. General Description

In *Liburnia furcifera* both the sexes are macropterous. The females are slightly bigger than the males and measure 4 mm., while the males measure only 3 mm. (both the measurements include the tegmen). They are almost ochraceous in colour on the dorsal surface except on the pronotum. There is a creamy white longitudinal area included in the lateral carinæ of pronotum, with the remaining part black. The tegmina are subhyaline, tinted with brownish ochraceous, which assumes a little darker tint apically and also just beneath the fused first and second anal veins. On the ventral side, the male is dark brown in colour while the female is ochraceous, thus showing that in *Liburnia furcifera* sexual dimorphism is noticeable.

IV. Head and Thoracic Region

The head (Fig. 1) is opisthognathous and the mouth parts do not warrant any attention as they are the typical Hemipterous type, *i.e.*, a piercing and sucking type. The carination of the head and thoracic regions are of some importance in classification, as the earlier workers on Homoptera

have invariably made use of them in distinguishing the species. At the same time this has given rise to many comr lications as 'there is considerable variation in this character' (Muir, 1915).

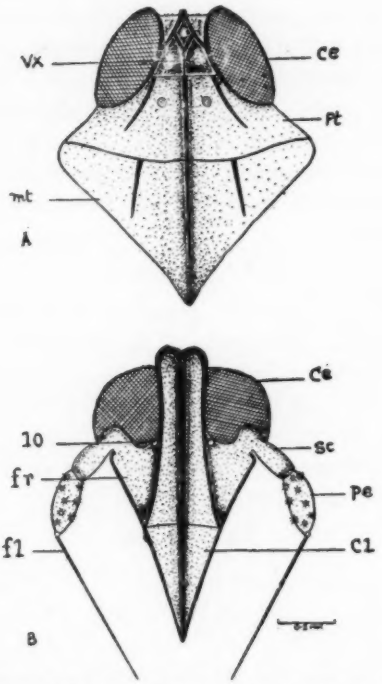

FIG. 1. (A) Dorsal view of head, pronotum and mesonotum. (B) Ventral view of head *ce*, compound eye; *cl*, clypeus; *fl*, flagellum; *fr*, frons; *lo*, lateral ocellus; *mt*, mesonotum; *pe*, pedicel; *pt*, pronotum; *sc*, scape; *vx*, vertex.

The clypeus, which is situated ventrally, is a small triangular sclerite that is distinctly tricarinate. Anterior to it is located the frons, which is five carinate. The outermost carinæ terminate at the region of the antennal sclerites, while the remaining three continue anteriorly up to the vertex. Of the five carinæ of frons, the middle one is the stoutest and there is a gradation in thickness from the middle towards either side. The vertex is longer than broad with the apex slightly narrower than the base. The middle carina of vertex bifurcates into two at its base, a distinguishing feature of the genus *Liburnia*. Immediately posterior to the bifurcation there are two small carinæ bounding a small area which appears as a depression in that region. Posteriorly, the vertex is characterised by the presence of two

pentagonal areas, separated by a faint medio-longitudinal carina. These two areas are slightly depressed. The two lateral carinæ of the vertex become apposed to the upper edge of the compound eyes and disappear posteriorly in the area of the pronotum. The prontoum is tricarinate and the lateral carinæ gradually fade before reaching the posterior edge of pronotum. The middle one, even though it narrows down posteriorly, is quite pronounced in its thickness and is continued into the median carina of the mesonotum. Anteriorly two pit-like depressions are observable, one on either side of the median carina. On the mesonotum there are three carinæ, of which the middle one is quite prominent and reaches the posterior margin, while the lateral ones are faint and fade off before reaching the posterior edge.

V. ANTENNÆ

The antennæ (Fig. 1, B) arise from the antennal sockets and extend well beyond the clypeus. The scape is almost equal to the pedicel, which bears a number of tubercles around it. The terminal division, namely, the flagellum, is bristle-like and tapers to a point distally. It is more than one and a half times the length of the scape and pedicel put together. One of the characteristic features of the antennæ of the genus *Liburnia* is that the scape and the pedicel are of equal length.

VI. WINGS

Metcalf (1913) published an account of the wing venation of certain families of Fulgoroidea. A decade later, Muir (1923) observed that the vein associated with the claval suture was the second main branch of the cubitus and that the so-called 'Y' vein of Fulgoroidea was formed by the union of the first and second anal veins. He, however, regarded the costal vein as the humeral branch of the sub-costa, which is not borne out by observed facts. Fennah (1944) categorically rejected it on two grounds; firstly, "it is under the onus of demonstrating how the supposed humeral vein acquired in Fulgoroidea the same relationship to the humeral plate as the costal vein bears it in other orders of insects" and secondly it would necessitate the conclusion that the costal vein and in certain families, even the costal cell, have also been lost by specialisation. If this view is accepted the region in front of the marginal vein is the 'costal cell' and consequently the reduction or disappearance of it indicates an evolutionary trend. Thus Flatidæ and Ricaniidæ, where the 'costal cell' is present, are more primitive than Cixiidæ and Tettigometridæ, where it is absent. Muir (1923) himself disagreed with this conclusion since he has stated that the more primitive type of venation of Homoptera is found among the Cixiidæ.

All the specimens of *Liburnia furcifera*, we were able to procure, were macropterous with an almost hyaline tegmen. The wing venation is comparatively well developed. Unlike that of certain Fulgoroidea, such as the members of the families Flatidae and Ricaniidæ etc., there is no precostal region. In the tegmen (Fig. 2) the costa is marginal and simple and is followed by a two branched sub-costa. The subcostal and costal veins form a common stalk basally. Radius is coalesced with sub-costa for nearly half of its length, and basally the first axillarly is fused with the second one.

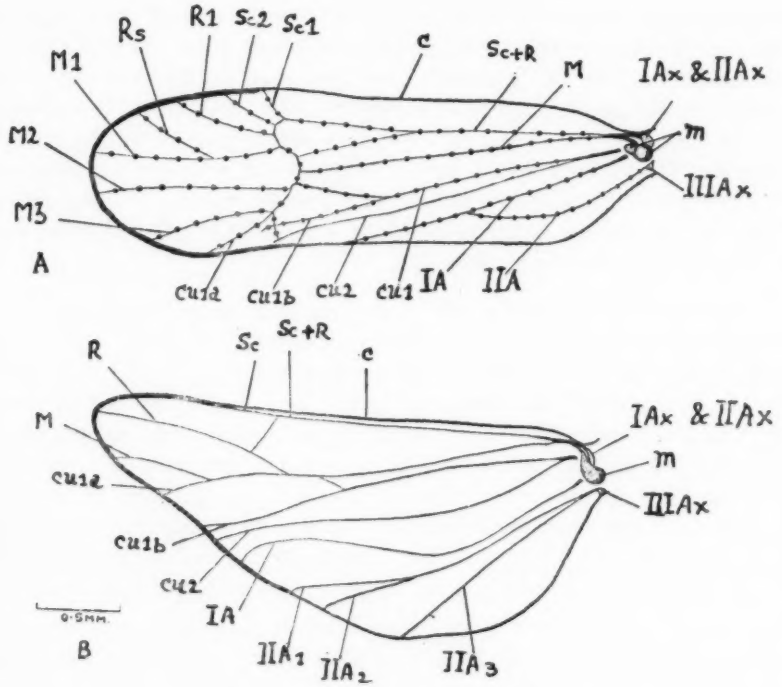

FIG. 2. (A) Venation of tegmen. (B) Venation of hind wing.

I *A*, II *A*, first and second anals; II *A*1, II *A*2, II *A*3, first, second and third branch of second anal; I *Ax* and II*Ax*, fused first and second axillaries; III *Ax*, third axillary; *c*, costa; cu 1, cu 2, first and second cubitus; *cu*1*a*, *Cu*1*b*, first and second branch of first cubitus; *m*, median plate; *M*, media, *M*1, *M*2, *M*3, first, second and third branch of media; *R*, radius; *R*1, radial one: *Rs*, radial sector; *Sc*, subcosta; *Sc* 1, *Sc* 2, first and second branch of subcosta; *Sc* + *R*, subscota *plus* radius.

The radius is two-branched, representing the radial 1 and radial sector. Media is three-branched, namely, media 1, media 2 and media 3. According

to Metcalf (1913) media 3 is formed by the union of media 3 + media 4 during the course of its development. The medial plate is intimately approximated with the base of the fused first and second axillaries. Cubitus is two-branched, namely, the cubitus 1 and cubitus 2. Further, cubitus 1 in its turn splits up into cula and culb. Basally the two cubital branches unite on a common elongated stalk. Posterior to cubitus 2 lies the first anal vein which independently springs from the basal sclerite. The second anal vein, which also springs independently from the base and runs parallel, joining the first anal a little posterior to its middle, and the union of the two anal veins gives rise to the characteristic 'Y' vein of the Fulgoroidea, which is distinctive of all Fulgoroidea, according to Imms (1957). The first anal represents the post-cubitus of Snodgrass (1935) as it has an independent origin and it does not fuse either with the base of the cubitus or with the third axillary. As the revised nomenclature of Snodgrass (1935) in respect of the cubito-anal region has not met with general acceptance, the present authors prefer to retain the old name, cubitus 2. A noteworthy feature of the tegmen is the presence of macrotrichiæ all along the course of veins except on the cubitus 2.

The striking features in the hind wing are the enlarged anal region, the reduced number of veins in respect of subcosta and media, and the complete absence of macrotrichia on the veins. The costa is marginal and the subcosta is unbranched. Both the radius and media are united basally. The radius is unbranched. The media is also unbranched and considerably reduced. The cubital vein is divided into two branches as in tegmen, and the cubital 1 in its turn splits into Cu 1*a* and Cu 1*b*; the Cu 1*a* coalesces with the media for almost its entire length being separated only near the marginal region (Metcalf, 1913). In the hind wing the first anal is unbranched, while the second anal is three-branched covering the enlarged anal area.

VII. LEGS

The fore and middle legs are similar to other Fulgoroidea. The hind leg (Fig. 3) bears the spur or calcar on the tibia which is important, as it is on this character the family is distinguished from other members of the superfamily Fulgoroidea. The shape of the spur is also an important factor, as the division of the family into sub-families is based on it (Muir, 1915). Its significance in taxonomy was first pointed out by Kirkaldy (1907) and later by Crawford (1914). In *Liburnia furcifera* the spur is foliaceous with a large number of teeth on the hind margin (the number varying from 25–30). The calcar gives the appearance of a lanceolate stipule toothed

along one edge. The foliaceous nature of calcar is regarded as the most advanced type by Muir (1915).

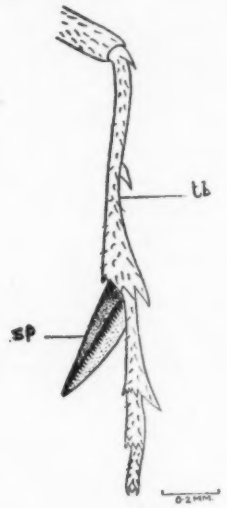

Fig. 3. Hind leg.
sp, spur; *tb*, tibia.

VIII. Genitalia

The taxonomy of Araeopids is complicated and there is as yet no complete key for the separation of all the known genera. Most of the taxonomists such as Kirkaldy (1907), Muir (1915), Giffard (1921) and Metcalf (1943), have stressed the importance of the male genitalia for an accurate system of classification of the family. Unfortunately few have studied in detail the male genitalia of the Indian forms, except Muir (1921, 1922). Distant (1906, 1916) a pioneer worker in this field did not extend his studies to the genitalia.

In the present description of the male genitalia, the terminology of Giffard (1921) and Hassan (1948) has been employed. The ninth segment in *Liburnia furcifera*, as in all Araeopids, is modified into a more or less chitinous ring, the pygofer (Fig. 4), in which no clear trace of tergum, sternum or pleurite is noticeable. The pygofer is rather elongated and is easily distinguishable from the other abdominal segments by its large size. It is dark brown, almost black, in colour. The opening of pygofer is longer than broad. Its posterior edge is more or less deeply emarginated, being

termed as the anal emargination. Out of this there projects a small tube-like structure, the anal segment of Giffard (1921), the result of the fusion of the tenth and eleventh abdominal segments. A more or less chitinous wall—the diaphragm—divides the pygofer into an inner and an outer chamber.

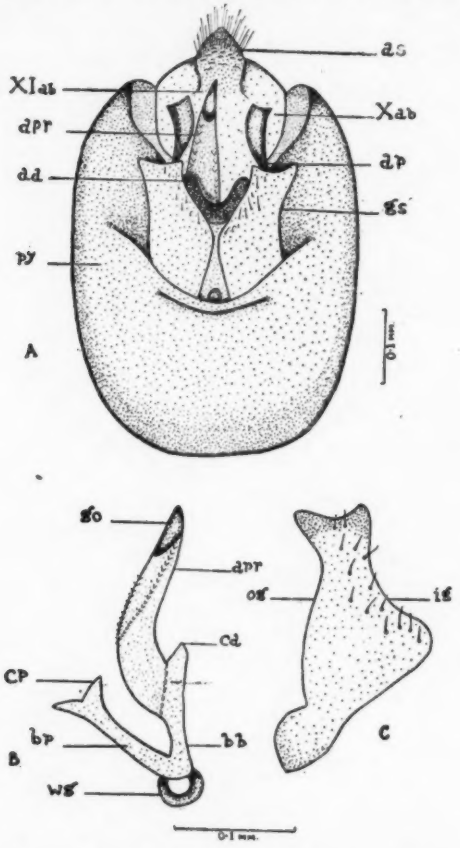

FIG. 4. (A) Pygofer. (B) Aedeagus with the basal plates. (C) single genital style.

ad, armature of diaphragm; *ap*, anal process; *apr*, aedeagus periandrum; *as*, anal style; *bb*, basal plate bridge; *bp*, basal plate prolongation; *ca*, connection to tenth abdominal segment; *cp*, connection to genital styles; *go*, gonopore; *gs*, genital style; *ig*, inner margin of genital style; *og*, outer margin of genital style; *py*, pygofer; *wg*, wing; *Xab*, tenth adbominal segment; *XI ab*, eleventh abdominal segment.

The dorsal margin of the diaphragm is 'V'-shaped, through which the anal segment passes out. In the middle of the diaphragm there is a highly chitinised region, the armature (*ad*). On either side of the ventral margin of

the pygofer project a pair of plate-like sclerites, known as the genital styles (*gs*). Their basal parts are hidden inside the pygofer. The genital styles are of a peculiar scapula-like shape being somewhat rounded at the base, rather abruptly bulged in the middle—the bulge being prominent on the inner side—and ending distally in a bifid head (Fig. 4 *c*). The styles are provided with minute hairs distally. The aedeagus arises from behind the diaphragm, and when at rest its apex projects above the middle of the dorsal margin of the diaphragm just above the armature. It consists of an ejaculatory duct surrounded by a sheath and passes right through a long chitinous tube, the aedeagus periandrum (*apr*). The aedeagus is spindle-shaped and opens terminally at the gonopore (*go*). On the lateral margins of the periandrum there are two rows of spines, one of which extends to the terminal portion, while the other stops rather short of it. The aedeagus is supported at the proximal end by chitinous plates, the basal plates of Pruthi (1925). The basal plates have a chitinous bridge called the basal plate bridge (*bb*) bearing a sclerotic ring, the wing of the basal plate bridge (*wg*). The basal plate is connected with the genital styles by a sclerite, termed the basal plate prolongation (*bp*), which is bifurcated distally—an arrangement which enables the insect to move the genital styles along with the aedeagus.

The tenth and eleventh abdominal segments are, as already mentioned, fused to form a single structure. The anal segment of Giffard (1921) consists of the tenth abdominal segment with its appendages as two divergingly curved processes called the anal processes (*as*), and the anal segment proper —the eleventh abdominal segment—with its posterior conical projection, the anal style (*as*). The anal style is wrinkled and beset with hairs.

IX. Summary

The present paper gives an account of the external morphology of *Liburnia furcifera* (Horvath):—

(1) The clypeus is tricarinate and the frons five-carinate. The middle carina of vertex bifurcates at its basal region and there are two pentagonal areas towards the posterior side.

(2) The antennæ extend well beyond the clypeus with the scape equal to the pedicel.

(3) In the tegmen, the costa is marginal and the subcosta is two-branched. The radius is two-branched and coalesces with the subcosta for about half of its length. Media is three-branched, cubitus and the anals are two-branched, and the two anals fuse to form the 'Y' vein. In the hind wing, the costa as well as the subcosta are unbranched. The radius coalesces

with the subcosta for most part of its length, and passes on unbranched. The cubitus as well as the anal veins are two-branched and the second anal in its turn is three-branched.

(4) In the case of the legs, the hind tibia carries a spur, which is foliaceous with 25–30 teeth.

(5) The male genitalia have been studied. The opening of pygofer is longer than broad, and there is a well-developed armature on the diaphragm. The genital styles are simple. The aedeagus is spindle-shaped with two rows of spines on the periandrum. The tenth abdominal segment bears a pair of anal processes and the eleventh one an anal style.

X. ACKNOWLEDGMENTS

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SOME FACTORS INFLUENCING THE EFFICIENCY OF *GONIOZUS MARASMI* KURIAN, A PARASITE OF THE MAIZE AND JOWAR LEAF ROLLER

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Received December 23, 1960

Introduction

The damage caused to *jowar* plants by the *maize* and *jowar* leaf roller [*Marasmia trapezalis* (Gucn.)] and the occurrence of its natural enemies in Delhi have been recently reported by the present authors (1961). *Goniozus marasmi* Kurian* (Hymenoptera: Bethylidæ) is a dominant parasite in the biotic complex of *Marasmia*. This parasite is usually met with in leaf rolls of *Marasmia* caterpillar in the field. It prefers caterpillars of medium size for oviposition, fully developed hosts being rarely attacked. The parasite was first noticed in *jowar* fields in the beginning of July, when the pest population was quite low. Towards the end of August, about 45% of the *jowar* plants in the field were found attacked by the leaf roller; an estimation of parasitism during this period showed that about 40% of the host caterpillars were attacked by *G. marasmi*. The natural parasitism, thereafter, steadily increased and by October about 60% of the caterpillars were parasitised.

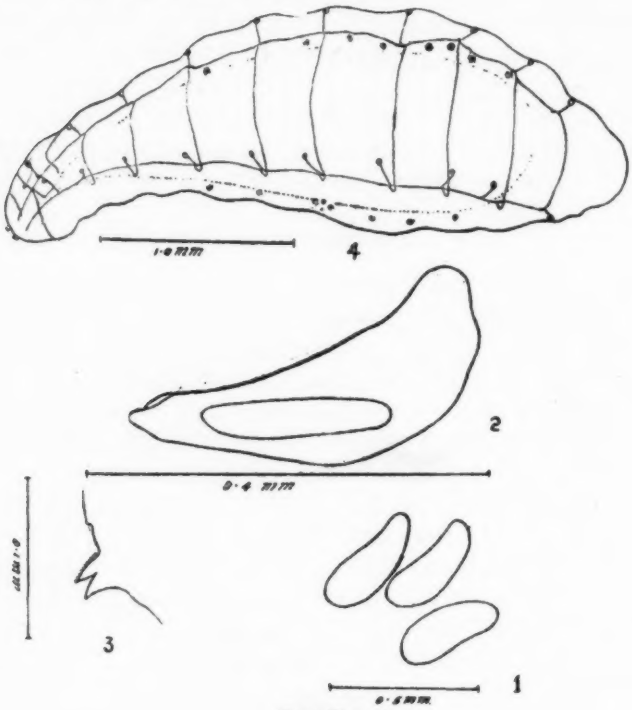
The observations recorded herein mainly concern an analysis of factors which modify the efficiency of *G. marasmi* as a natural mortality factor in populations of *Marasmia*. Careful observations were carried out periodically to study the interactions occurring between individual members of the *Marasmia* complex in nature. Laboratory experiments on parasite behaviour were also done at a temperature of 80° F. and 75% relative Humidity, to correlate laboratory data with field observations. The results of these studies are incorporated in this communication.

Biology, Bionomics and Habits

The egg is elongate-ovoid and slightly curved (Plate XIII, Fig. 1). It is transparent and glistening when newly laid and is not easily distinguished

* Identified by Dr. C. Kurian, Central Cocoanut Research Station, Ochira, Kerala State.

from the cuticular folds of the host. The incubation period lasts for 18–24 hours under laboratory conditions.

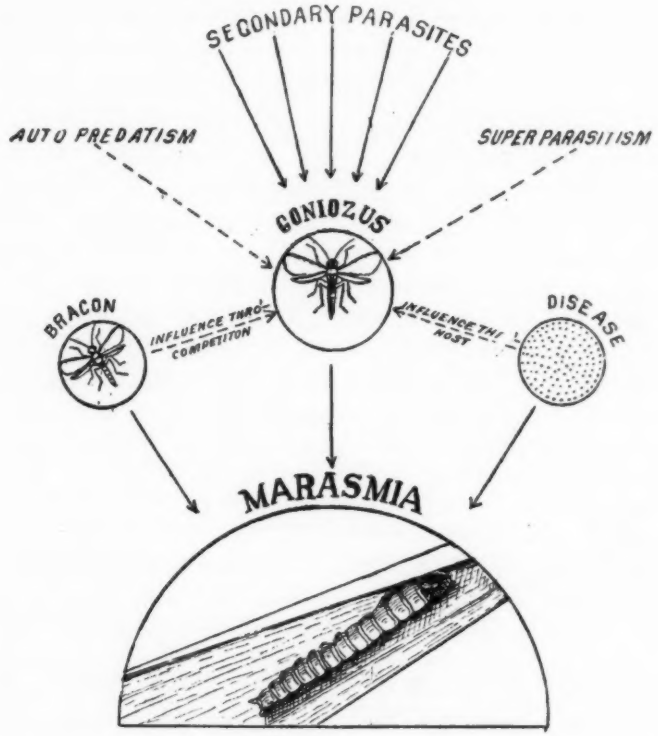


TEXT-FIG. 1

As soon as the egg hatches, the parasite grub starts feeding on the host and remains at the same point throughout the feeding period. The grub is arched and more or less takes the shape of the curvature of the host (Plate XIII, Fig. 2). In the very early stage the body segmentation is indistinct (Plate XIII, Fig. 2). Very soon the spiracles and the tracheal system appear. As the larva develops, its body becomes more curved. In a 42-hour old larva, 13 body segments and 10 pairs of spiracles can be clearly seen (Plate XIII, Fig. 4). The mandibles are well developed (Plate XIII, Fig. 3). The cuticle of the grub is very thin and transparent and the internal organs are clearly visible. The larval stage lasts for 48 hours.

When full fed, the grubs leave the host, drop down on the leaf and spin brownish cocoons near the host remains or a little away in the leaf roll. By the time the grubs become full fed, the host is practically dead, showing

only slight tremors of the head and legs. The pupal period lasts from 5–6 days. The total life-cycle is about 8–9 days: egg period, 1 day; larval period 2 days; and pupal period 5–6 days.



TEXT-FIG. 2. Diagrammatic representation of the various factors that influence the efficiency of *Goniozus marasmi* Kurian.

MODE OF PARASITISM

When a female parasite encounters a host, it seizes the body of the latter with the mandibles and gets a firm grip on the thoracic region. The caterpillar tries to shake off the parasite but the hold of the parasite is so firm that it succeeds in overpowering the host. When the host is thus brought under partial control, the parasite brings the tip of the abdomen under the body of the caterpillar and instals a sting ventrally just in front of the first pair of thoracic legs. The caterpillar is paralysed instantaneously. It then begins to examine the body of the host thoroughly by means of its

mandibles and extruded ovipositor, apparently to make sure that the host is healthy and does not contain any parasite stages. If the host is already parasitised with eggs or early instars of *G. marasmi*, the parasite first feeds on them and thus destroys them, before laying eggs. In several cases, caterpillars collected in the field had evidence of eggs destroyed by the parasite.

OVIPOSITION BEHAVIOUR

After clearing the host of eggs and grubs already present, the parasite probes the body cuticle of the host with its extruded ovipositor. As soon as a suitable site is located, which is usually between two cuticular spines, the female remains motionless for a while, with the antennæ outstretched. The tip of the ovipositor is now pressed against the dorso-lateral region of the host, a pulsatory movement of the abdomen is visible, and the egg slowly descends down the ovipositor. As the egg comes out, it is glued transversely in the intersegmental groove of the host. The first egg is usually laid on one of the posterior abdominal segments, say the third or fourth from the anal end. After laying an egg, the female, remaining in the same position, tilts the abdomen to the opposite side and lays another. It then moves forward and lays two more eggs in the next segment in the same way. In this manner about 4–6 eggs are laid on a medium size larva. The time taken to attack and complete oviposition on a host is about 30 minutes. The paralysed host recovers in about 30–40 minutes and continues to feed and move about till the grubs stop feeding. In some cases the caterpillar has been observed to spin a thin cocoon after the eggs on it have hatched.

SOME ASPECTS OF PARASITISM AND FACTORS WHICH TEND TO MODIFY PARASITE EFFICIENCY

Superparasitism.—The number of *Goniozus* eggs or grubs on a single host varies from 1–12. In one host caterpillar, collected from the field, as many as 12 early instarts were recorded. However, all of them did not complete development as the survivors had outgrown and pushed aside the weak ones; of the survivors that succeeded in pupating, 5 emerged as apparently normal adults, the rest turning into 'runts' with poorly developed wings. When superparasitism is highly pronounced, the resulting cocoons are whitish, thin and lack the brownish tinge. The normal number of grubs which can successfully develop in a medium size caterpillar is about 6.

Multiparasitism.—In the experimental fields at New Delhi *M. trapezalis* is also found attacked by a braconid (*Bracon* sp.), in addition to *G. marasmi.*

In many cases, the caterpillars are attacked by both the parasites simultaneously. As many as 6 grubs of *Bracon* and 4 of *G. marasmi* were found together on a single host, collected in the field; this resulted in the death of the host as well as the parasites. However, when the number of grubs present on a host is low, *Bracon* completes its development and emerges successfully while *G. marasmi* is eliminated. *Bracon* attacks hosts that are already parasitised by *G. marasmi*, while the latter avoids those parasitised by the former. *Bracon* seems to be intrinsically superior to *G. marasmi*.

Secondary parasitism.—Five different species of secondary parasites are found to attack *Goniozus marasmi* is its pupal stage. These are: 1 species of an Elasmid, 1 species of a Ceraphronid, 1 species of a Eurytomid and 2 species of Eulophid.

Microbial Disease of the Host

Several larvæ of *Marasmia* collected in the field are found attacked by a disease caused by a pathogenic microorganism. Some of these diseased ones are found to contain eggs or early grubs of *G. marasmi*. The parasite grubs invariably died when the diseased caterpillar succumbed to the disease. In such cases, the host caterpillars which are apparently healthy, are already infected with the disease organisms at the time of parasitisation.

Discussion

The populations of *Marasmia trapezalis* in *jowar* and *maize* fields are affected by various biotic and physical mortality factors. Among the biotic factors, the parasites *Goniozus marasmi* and *Bracon* sp. appear to be the main natural mortality factors which provide fluctuations in host populations. Of the parasites, *G. marasmi* seems to play a dominant role in the natural control of the pest. Laboratory studies and field observations have revealed many interesting features of parasitism and some of the possible ways in which the efficiency of *G. marasmi* is affected in the field.

In the early instars of *G. marasmi* the body segmentation is indistinct, whereas in the final instar, 13 body segments and 10 pairs of spiracles are clearly visible. The larval stage remains sedantary, using a single feeding puncture throughout its development. The parasite grub, if once dislodged, is unable to reattach itself to the host. In several species of *Goniozus* and *Cephalonomia* the larval period is very short and is completed in 2 or 3 days (Clausen, 1940).

The mode of attack by *G. marasmia* has certain distinctive features. Clausen (1940) states that stinging in the thoracic region is for paralysing

the mandibles and the legs of the host; in *Sclerodermus chilonellæ* repeated stinging takes place and the later insertions are in the abdominal region; in *Lælius anthrenivorus*, the female after stinging, chews the throat of the host probably to injure the thoracic ganglion, and the process of paralysing the host takes several hours. But *G. marasmi* brings about the paralysis of the host with one stab, ventrally in front of the first pair of thoracic legs. The habit of paralysing the host quickly with one stab is an important feature of *G. marasmi* in that it can attack and paralyse several hosts within a short time especially when the host density in the field is high.

A very interesting observation made in the course of the present studies is the feeding habit of the adult parasite. In the laboratory it was found that if a parasitised host containing eggs or early instars of its own species was exposed to a gravid *Goniozus* female, the latter invariably fed on the eggs and grubs before ovipositing. This phenomenon of 'autopredatism,' if we may term it so, appears to be unique and is an important factor of practical importance. Wheeler (quoted by Clausen, 1940) mentions that *Sclerodermus macrogaster* sometimes eats its own eggs, though not the larvæ, and this he believes, is to regulate the size of the brood. *G. marasmi* destroys the eggs and grubs evidently to safeguard the interests of its own progeny. If 'autopredatism' takes place in nature—it is possible that it does happen—then it may influence parasitism in the field and lower the efficiency of *G. marasmi*. In nature, 'autopredatism' may occur if the parasite is in abundance and host population is low.

In Bethylidæ, the position of eggs on the host is found to vary. It is ventrally on the thorax in *Prorops nasuta*, at the side in *Parascleroderma berlandi* Man., and transversely in the intersegmental grooves of the mid-dorsal region in several species of *Goniozus* (Clausen, 1940). Cherian and Israel (1943) report that *G. indicus*, a parasite of the sugarcane borer, lays eggs on the dorsal, ventral and lateral sides of the body of the host but oftener on the ventral and lateral sides. They further state that the eggs are laid singly at an interval of 2–5 minutes in the folds of the intersegmental groove. In *G. marasmi*, the eggs are placed transversely in the intersegmental grooves, dorso-laterally between two cuticular spines. Very rarely the eggs are deposited dorsally or in the thoracic segments. The first two eggs are laid in the posterior abdominal segment, the next two in the segment just in front and so on. Clausen (1940) mentions that among gregarious forms the eggs are placed transversely, while in solitary forms they lie longitudinally.

Although many of the Bethylids paralyse the host permanently, members of the genus *Goniozus* are an exception (Taylor, 1933). The host of *G. claripennis* Foerst. recovers within two hours after being stung (Voukassovitch, 1925). The host caterpillar paralysed by *G. marasmi*, however, recovers within 30–40 minutes after stinging and continues its normal activities and some of them even spin a thin cocoon inside the leaf-roll. Cherian and Israel (1943) do not mention anything regarding the fate of the paralysed host caterpillar attacked by *G. indicus*.

Direct feeding of adults on the punctures of the host has not been observed. According to Bridwell (1919, 1920), all members of the *Goniozus* group feed on sugary fluids only. The feeding by adult parasites occasionally on its own eggs and grubs may provide them with sufficient food nutrient for egg development.

The more important factors that influence the efficiency of *G. marasmi*, are superparasitism, multiparasitism, secondary parasitism, and the disease affecting the host. When there is a superabundance of parasite grubs on a host, all of them do not complete their development, some are, in fact, pushed aside by the more sturdy grubs and are thus killed as a result of competition; the adults that emerge are smaller than the normal ones, some of them turning into 'runts'. Clausen (1940) mentions that there is considerable variation in size among individuals of Bethylids which develop on a single host, due to crowding.

Multiparasitism by *G. marasmi* and *Bracon* sp., on *M. trapezalis* results either in the death of the host and consequently of both the parasites, or in the death of the host and *G. marasmi*, depending upon the degree of parasitism. It is important to note that in either case *G. marasmi* succumbs, proving the superiority of *Bracon*. The death of *G. marasmi* may be due to feeding on the body contents of the host already paralysed by *Bracon* sp.

It is disquieting to note that as many as 5 different species of secondary parasites attack *G. marasmi* and thus reduce the effect of total parasitism of host population by this parasite. Another important factor that limits the efficiency of *G. marasmi* is the microbial disease affecting the host. When the host dies as a result of the disease, the parasites on it are also killed and thus the efficiency of the parasite is modified considerably.

In spite of these various factors (Text-Fig. 2) that may adversely affect the parasite efficiency, up to 60% parasitism by *G. marasmi* was observed in the field. It only shows that *G. marasmi* plays a very important role in the natural control of *M. trapezalis* and has great potentialities.

The factors mentioned above are not to be regarded as exhausting the possibilities in this particular direction, but may be regarded as important ones for modifying the efficiency of *G. marasmi* in nature. It must, however, be borne in mind that parasite efficiency in the field cannot be modified by a single factor. The relative influence of the various factors are bound to vary from point to point in the environment and it is the complex of all the factors, taken as a whole, which produce such effects.

SUMMARY

1. The present investigation deals with an analysis of the factors which modify the efficiency of *Goniozus marasmi* Kurian, a dominant parasite of the biotic complex of *Marasmia trapezalis* (Guen.), at New Delhi. An attempt is made to correlate field observations with laboratory data on the biology and bionomics of the parasite.

2. The parasite has a short life-cycle which is about 8–9 days under laboratory conditions.

3. Unlike other members of the Bethylidæ, *G. marasmi* bring about the paralysis of the host with one stab and within a very short period; this enables the parasite to attack and paralyse several hosts in the field within a short time.

4. The parasite feeds on the eggs and grubs of its own species. The term 'autopredatism' has been suggested for this phenomenon. 'Autopredatism' may lower the efficiency of *G. marasmi* in the field.

5. The thin cocoon spun by some of the host caterpillars after the hatching of the parasite eggs on them, may protect the parasite grubs from 'autopredatism,' and the host from the attack by *Bracon* sp.

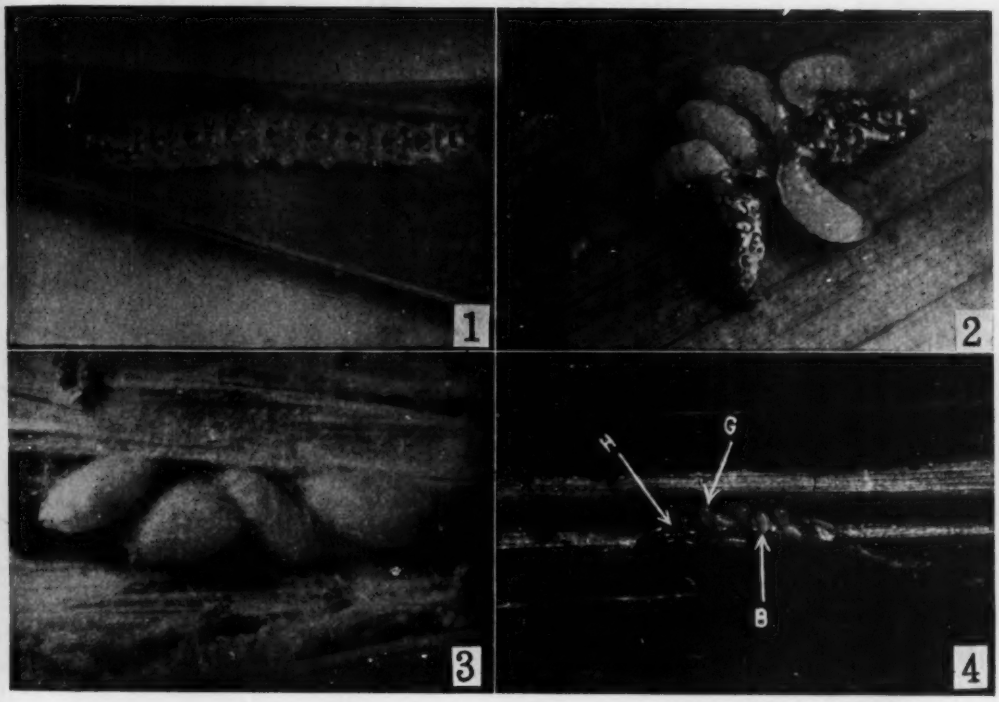
6. The more important factors that influence the efficiency of *G. marasmi* are:

(*a*) Superparasitism—as a result of competition, some grubs are killed, while others turn into 'runts'.

(*b*) Multiparasitism—when the host as well as *G. marasmi* are killed, and *Bracon* sp. survives.

(*c*) Secondary parasitism—5 different species of secondary parasites attack *G. marasmi* and reduce its efficiency.

(*d*) Microbial disease affecting the host—the disease kills the host as well as the parasite stages present on the host.



FIGS. 1–4

FIG. 1. Parasitised *Marasmia* caterpillar showing position of *Goniozus* grubs feeding on host.

FIG. 2. Full-fed *Goniozus* grubs on the host which is about to succumb to the attack by the parasite.

FIG. 3. Cocoons of *Goniozus* in jowar leaf roll.

FIG. 4. Multiparasitism—both *Goniozus* (G) and *Bracon* (B) grubs feeding on the same host (H).

7. In spite of several adverse factors that seem to lower the efficiency of *G. marasmi*, a parasitism of up to 60% was observed in the field when the pest population was highest. Hence, this parasite may be considered as a potential natural agent in the control of *Marasmia trapezalis*, when conditions are favourable.

Acknowledgements

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NUTRITIONAL REQUIREMENTS OF THE LARVA OF RICE MOTH, *CORCYRA CEPHALONICA* (STAINT.)

Studies on Feeding Response to Various Natural Foods[1]

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Corcyra cephalonica, popularly known as the rice moth or sometimes the 'flour moth' is a serious pest of stored grains. The adult moth is grey in colour and does not feed. The larva, however, constructs a feeding tube or gallery consisting of silken web and food particles. It remains inside this gallery where it feeds and grows. The larva at 30° C. and 70% relative humidity takes about 28 days to pupate and the moths start emerging a week after pupation (Uberoi, 1959).

The earliest reference to this moth was made by Stainton (1866) who named it *Melissoblaptes cephalonica*. Later, Ragonot (1885) gave it the generic name, *Corcyra*. The only recognized species of this genus is *cephalonica*. Ayyar (1919) made the first record of *Corcyra cephalonica* occurring on rice and meal of all cereals in this country. Recently Rao (1954) has published a report which deals, among other observations, with feeding tests on *Corcyra* larva with a variety of foods. In this paper Rao has summarized a number of scattered reports of earlier workers referring to the range of food materials used by this insect. Many of the earlier observations including that of Rao (1954) are incomplete in many respects and an adequate explanation of the feeding behaviour of this insect is not available.

The present investigation records the feeding behaviour of *Corcyra* on various natural plant products and aims at establishing a correlation between the food and the food requirements of this insect. The observations cover the feeding trials with a large variety of commodities with an emphasis

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[1] From a *Doctoral Thesis* approved by the University of Delhi, India.

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on the *physical state* of the food materials offered. Unlike the procedure adopted by Rao (1954), freshly hatched larvæ were used in the feeding experiments under the controlled conditions of temperature and relative humidity (Rao used the eggs). The results have been discussed in the light of basal food requirements of this insect.

Material and Methods

A culture of *Corcyra* was maintained in the laboratory on coarsely milled sorghum (Jowar) at 29–30° C. and 70% relative humidity. Care was taken to keep the general conditions of the culture uniform specially in regard to the quality and quantity of food, temperature and insect population. Freshly hatched (0–24 hr. old) larvæ were used in the experiments. They were obtained from eggs collected from a specially designed cage in which the moths could mate and oviposit. The larvæ, which hatch after an incubation period of 4 days (90–96 hr.), were picked up with a trimmed soft camel hair brush and transferred to feeding bottles containing 10 gm. of material with 100 mg. of M. nipagin (Methyl *para*-hydroxy benzoate), a micro-organism inhibitor. Three bottles were denoted to each kind of food material and ten freshly hatched larvæ were introduced into each bottle. The efficiency of a food was assessed on the basis of 'growth index' calculated by dividing figure *n* (representing percentage of adults which emerged) by figure Av. (representing average period of development).

All tests were conducted at 30° C. and 70% relative humidity. The feeding trials were conducted in the following way:

(i) Various cereals and millets offered in different physical forms, *i.e.*, whole grain, broken grain and flour (60 mesh).

(ii) Various pulses given (as above) in different physical forms.

(iii) Oil-seeds offered both whole and in crushed form.

(iv) Spices and other food-stuffs offered whole and as coarsely powdered seeds or fruits, etc.

The results of growth response of larvæ to the various commodities were compared with those obtained from broken sorghum. Investigations of the author have demonstrated that certain other media like broken wheat and flour of pearl millet (*Pennisetum typhoides*) have a better nutritive value.

Experimental

Development on cereals and millets.—The results of feeding trials with wheat show that growth was very satisfactory when this cereal was offered

in the form of broken grain, and the growth index (2·00) excelled that obtained with broken sorghum. Whole wheat, on the other hand, proved a poor feeding medium for the larva. Wheat-flour also was good for the growth provided it was of suitable extraction. Growth index decreased with increase in extraction (decrease in size of particle) of wheat-flour. The growth index with flour passed through a 40-mesh sieve was almost double that passed through a 80-mesh.

Whole rice proved almost of the same nutritive value as broken sorghum. Rice flour was inadequate for growth. Of the three different physical forms of sorghum offered to the larva, the growth, both on whole grain and flour, was much inferior to that on the broken grain of this cereal. The feeding behaviour of larva with maize was interesting. All the three different physical forms, were almost of the same nutritive value and proved fairly satisfactory. Growth response to barley, when offered as whole grain, was very poor as compared with flour which supported normal growth.

The results obtained with pearl millet were striking. The growth on whole grain of this millet was better than that on broken grain of sorghum, while it was excellent when pearl millet was offered in the form of flour, the latter being distinguishable as a medium with the highest value of growth index ever recorded in these experiments.

Comparison of the food values of various cereals and millets shows that the flour of pearl millet and broken grain of wheat proved the most satisfactory feeding media, superior even to sorghum. It may be mentioned that the superiority of wheat bran to sorghum for mass rearing of *Corcyra* had been indicated by Murthi and Rao (1945). So far as the comparison between the nutritive values of the whole grain and flour of any particular cereal or millet is concerned, there is not much indication of any definite preference exhibited by the larva. Growth on the whole grain of wheat, barley or pearl millet was inferior to that on these commodities when offered in flour form. In the case of rice or sorghum however, the whole grain proved better than the flour.

Development on pulses.—Chick pea (*Cicer arietinum*), both in broken and flour forms supported adequate growth but its whole grain proved of little nutritional value. The result of feeding trials with black gram shows that the whole grain of this pulse did not support any growth at all and its flour too formed an unsatisfactory feeding medium. In the case of green gram, like chick pea, growth on broken seeds or on flour was normal, while its whole grain proved much inferior. Red gram or lentil offered in the form of broken grain or flour failed to support larval growth.

Development on oil-seeds and spices, etc.—Among the various oil-seeds tested, crushed cotton-seed proved the most satisfactory medium for growth. Groundnut, almond and mustard seeds were inadequate. Castor seed and coconut kernel proved entirely unsuitable to sustain life.

The spices, *viz.*, coriander, fennel, black pepper, caraway, turmeric and cummin, offered as seeds or coarse powder were found to be unfavourable media for the development of the larva. Broken seeds of fenugreek, however, promoted a slight growth. But the most striking results were obtained with chilli powder which proved a fairly satisfactory medium, comparable to the broken grain of sorghum (control). Growth on poppy seeds or pomegranate seeds was very poor.

Development on various feeding stuffs fortified with yeast.—Of the various cereals, millets, pulses, spices and other food-stuffs tested, those which either failed to support any growth or contributed only to partial growth were offered to the test insect in the form of flour mixed with 5% dried brewer's yeast. The experiments described elsewhere (Uberoi, 1959) refer to yeast as an adequate source of protein, minerals, sterol, fat-soluble factor and B-vitamins, essential for the normal growth of the larva of *Corcyra*. When supplemented with a suitable carbohydrate, yeast became an adequate medium for larval growth. The results of feeding the larva on various food-stuffs fortified with yeast show that an addition of the latter did not result in the improvement of the nutritive value of any one of the substances which had been found inadequate in the preceding trials. Whatever little growth occurred on these fortified media, was probably due entirely to the yeast because it has been shown (Uberoi, 1959) that yeast by itself could support some larval growth.

Discussion

The experiments detailed in this paper may be considered to lead to some definite conclusions. Various cereals and millets, *i.e.*, wheat, rice, sorghum, maize, barley and pearl millet in suitable physical state were readily accepted by the larvæ which were observed to normally feed, grow and become adults. Subramaniam and Rao (1940) and Rao (1954) in their reports on the results of feeding this insect with various edible stuffs concluded that broken seed of sorghum formed the most favourable medium for securing the highest rate of emergence in a minimum developmental period. The results of the present investigations show that out of all the cereals and millets tested, flour of pearl millet and broken grain of wheat have proved better rearing media than sorghum. Pearl millet which had not been tested by any of the earlier workers is a medium that is easily

TABLE I

Development of Corcyra *on various food-stuffs*

Food	% of larvæ becoming adult (*n*)	Average development period in days (Av.)	Growth Index	% of pupæ till the completion of the experiment	% of larvæ till the completion of the experiment
CEREALS AND MILLETS					
Wheat (*Triticum æstivum*)					
Whole	30·0	56·1 (40–75)	0·53	16·6	0
Broken	80·0	39·4 (31–56)	2·00	6·6	0
Wheat-flour					
40-mesh	70·0	41·1 (37–46)	1·70	0	0
50 ,, ...	60·0	43·7 (35–56)	1·37	0	0
80 ,, ...	50·0	56·3 (47–74)	0·88	23·3*	0
100 ,, ...	33·3	54·2 (50–59)	0·61	0	0
Rice (*Oryza sativa*)					
Whole	60·0	50·3 (42–64)	1·19	0	20·0
Flour (60-mesh)	40·0	68·4 (56–90)	0·58	10·0	23·3
Sorghum (*Andropogon sorghum*)					
Whole	43·3	50·0 (37–67)	0·86	0	0
Broken	60·0	45·0 (36–60)	1·33	6·6	0
Flour (60-mesh)	40·0	59·5 (49–71)	0·67	13·3	0
Maize (*Zea mays*)					
Whole	46·6	44·2 (29–70)	1·05	0	16·6
Broken	56·6	43·4 (33–60)	1·30	0	0
Flour (60-mesh)	56·6	51·1 (41–64)	1·10	13·3	0

Barley (*Hordeum vulgare*)						
Whole	16·6	60·0 (50–70)	0·27	6·6	6·6
Flour (60-mesh)	70·0	56·5 (47–75)	1·23	6·6	0
Pearl millet (*Pennisetum typhoides*)						
Whole	70·0	43·0 (34–52)	1·62	6·6	6·6
Flour (60-mesh)	83·3	35·5 (33–45)	2·03	0	0
PULSES						
Chick pea (*Cicer arietinum*)						
Whole	3·3	59·0 (59)	0·05	0	0
Broken	66·6	50·0 (42–64)	1·33	0	0
Flour (60-mesh)	66·6	46·1 (39–62)	1·44	0	0
Black gram (*Phaseolus mungo*)						
Whole	No survival	..	..	..	..
Flour (60-mesh)	30·0	78·4 (64–84)	0·38	3·3	13·3
Green gram (*Phaseolus aureus*)						
Whole	13·3	79·7 (57–97)	0·16	3·3	0
Broken	66·6	49·3 (43–56)	1·35	10·0	0
Flour (60-mesh)	56·6	49·6 (41–62)	1·14	0	0
Red gram (*Cajanus cajan*)						
Broken (husked)	No survival	..	..	..	..
Flour (60-mesh)	,,	..	..	..	..
Lentil (*Lens esculenta*)						
Whole (unhusked)	3·3	70·0 (70)	0·04	3·3	13·3
Broken (husked)	0·0	..	..	0·0	23·3
Flour (60-mesh)	No survival	..	..	..	..
OIL-SEEDS AND SPICES, ETC.						
Cotton-seed						
Whole	6·6	63·0 (62–64)	0·10	0	3·3
Crushed	70·0	52·6 (40–64)	1·33	0	3·3

TABLE I (*Contd.*)

Food	% of larvæ becoming adult (*n*)	Average development period in days (Av.)	Growth Index	% of pupæ till the completion of the experiment	% of larvæ till the completion of the experiment
Groundnut					
Pod	6·6	58·0 (57–59)	0·11	0	0
Seed (Whole)	30·0	44·2 (35–53)	0·67	16·0*	0
Seed (Crushed)	0·0	..	..	6·6	0
Almond seed					
Whole	36·6	50·2 (32–75)	0·72	0	0
Castor—Oil-seed					
Whole	No survival	..	..	..	..
Crushed	,,	..	..	..	..
Coconut kernel (Dried)					
Crushed	No survival	..	..	..	..
Mustard seed					
Whole	10·0	71·6 (68–75)	0·13	0	16·6
Crushed	10·0	72·0 (68–76)	0·13	0	0
Fenugreek seed					
Whole	No survival	..	..	..	..
Broken	46·6	77·3 (59–97)	0·60	6·6	0
Coriander seed					
Whole	3·3	70·0 (70)	0·04	3·3	0
Powder	No survival	..	..	..	..

Fennel seed				
Whole	0·0	..	..	0	16·6
Powder	No survival	..	..	..	..
Black pepper				
Whole	No survival	..	..	..	..
Powder	,,	..	..	..	..
Caraway				
Whole	No survival	..	..	..	..
Chilli				
Powder	73·3	55·3 (42–74)	1·32	0	13·3
Turmeric				
Rhizome	No survival	..	..	..	..
Powder	,,	..	..	..	..
Cumin seed				
Whole	3·3	62·0 (62)	0·5	3·3	0
Ginger				
Rhizome	No survival	..	..	..	..
Poppy seed				
Whole	30·0	69·5 (56–84)	0·43	16·6	0
Pomegranate seed				
Crushed	3·3	85·0 (85)	0·03	6·6	0
FOOD-STUFFS FORTIFIED WITH YEAST					
Black gram					
Flour	23·3	70·3 (59–78)	0·33	0	0

TABLE I (*Contd.*)

Food	% of larvæ becoming adult (*n*)	Average development period in days (Av.)	Growth Index	% of pupæ till the completion of the experiment	% of larvæ till the completion of the experiment
Green gram Flour	56·6	46·6 (39–54)	1·21	20·0*	0
Red gram Flour	3·3	92·0 (92)	0·03	3·3	0
Lentil Flour	0	..	..	0	6·6
Groundnut seed Crushed	0	..	..	6·6*	0
Castor seed Crushed	No survival	..	..	..	..
Mustard seed Crushed	6·6	62·5 (61–64)	0·10	0	0
Coconut kernel Crushed	No survival	..	..	..	..
Fenugreek seed Powder	0	..	..	0	3·3
Coriander seed Powder	0	..	..	3·3	3·3

Fennel seed Powder	..	..	..	..	No survival	..	..	..	..
Black pepper Powder	..	..	..	..	No survival	..	..	..	..
Caraway Powder	..	..	..	..	0	..	..	6·6	0
Cumin seed Powder	..	..	..	..	0	..	..	0	3·3

* Dead.

available. It may probably form a better medium for the mass rearing of *Corcyra* for the mass production of the hymenopterous parasites of the sugarcane-borers such as, *Trichogramma minutum* and *Bracon galechiæ*. However, the fecundity rates of moths emerging from broken wheat, pearl millet and sorghum would require experimental comparison.

The fact that the protein content of all the cereals and millets mentioned above varies between 8% and 12% and the carbohydrate content between 64·7% and 69·7% shows that this insect can flourish in media with a relatively low protein content. It may be mentioned here that yeast protein even at the low level of 2·5% was adequate for normal growth (Uberoi, 1959). It would therefore appear that it is the quality of the protein offered for feeding that is of great importance.

Poor growth response to black gram, red gram and lentil needs further elucidation. The moisture content of these pulses is almost the same as that of cereals. The low level of contents such as B-vitamins, salts, sterol, the fat-soluble factor or even protein does not appear to be the factor limiting growth, because addition of yeast did not result in any improvement. The particle size of the flour of these pulses was the same (60-mesh) as in any of the more satisfactory food-stuffs. The data on the carbohydrate content in pulses, so far as the quantity is concerned, are favourable for normal growth. So, the factors responsible for poor growth in the case of these materials should have been either the inferior quality of the carbohydrate or the presence of some growth-inhibiting substance in them. Singh and Pant (1955) also noticed a poor growth response on the part of *Trogoderma granarium* to pulses. Similarly Pant *et al.* (1957) indicated that some pulses were nutritionally inadequate for *Latheticus oryzæ*. According to Pal and Bose (1943), a diet consisting of one part of any one of the pulses mentioned above and two parts of rice was somewhat toxic to albino rats. They attributed the toxic effect to the pulse factor in the diet.

The results of feeding trials with oil-seeds present an interesting picture. Crushed cotton-seed, contrary to the findings of Rao (1954), is the only commodity which supported a normal growth of the larva. The superiority of crushed cotton-seed can be explained, to some extent, to be due to its chemical composition as indicated in Table II. It contains about 18% protein, 30% carbohydrates and 19% ether extracted (oil) material. In groundnut, almond and in coconut kernel, all of which contributed to a poor growth, the fat content is relatively high (44–59%) while the carbohydrate content is low (15–17·9%). The fact that there was no improvement in growth even when some of the oil-seeds were fortified with yeast, points

to the possible inadequacy of the carbohydrate content of some of these materials. However, the possibility of other factors, such as excess of ether extract or the presence of some toxic substance in these oil-seens, interfering with growth, cannot be ignored.

TABLE II

Chemical composition of some of the feeding materials

Name	Protein (%)	Ether extract (%)	Carbo-hydrate (%)	Reference
Wheat ..	12·1	1·9	69·0	Kent-Jones and Amos (1957)
Rice ..	8·3	1·8	64·7	Do.
Sorghum ..	10·7	3·2	69·7	Do.
Maize ..	9·9	4·4	69·2	Do.
Barley ..	10·5	1·5	66·6	Do.
Chick pea ..	23·4	1·1	54·3	Do.
Black gram ..	25·12	0·65	54·81	Ranganathan *et al.* (1937)
Green gram ..	26·36	0·73	52·68	Do.
Red gram ..	21·40	1·23	60·34	Do.
Lentil ..	25·5	1·9	52·2	Kent-Jones and Amos (1957)
Cotton-seed ..	17·9	19·4	29·9	Do.
Groundnut seed ..	26·8	44·9	17·5	Do.
Almond seed ..	21·8	47·3	17·9	Do.
Coconut ..	5·5	59·0	15·0	Do.
Poppy seed ..	20·9	32·5	23·3	Do.

In respect of spices and similar other food material, the results of feeding trials with chilli powder are worth noting. They indicate chilli powder,

which is used only as a condiment in human nutrition, is a complete food for the *Corcyra* larva. Rao (1954) recorded only insignificant growth on a diet of chilli powder, whereas the present investigations* indicate that this moth can be a destructive pest of stored chilli powder. It is, however, uncertain if this commodity forms a suitable medium for oviposition by the moth. Chilli powder has been found to be a good feeding medium for *Tribolium castaneum* also (Pant, 1959). As to the discrepancy between the results of the present investigation and those reported by Rao (1954), it may be pointed out that a true comparison cannot be made since it is not known whether all the eggs placed by Rao on various food-stuffs hatched into larvæ.

The data on the present feeding trials may now be summed up thus: the various food materials which become infested with *Corcyra* larvæ, vary in their ability to support body growth. The degree of infestation and a determination of whether *Corcyra* is a major or a minor pest of a particular commodity would largely depend upon the following factors:—

(i) The extent to which the chemical composition of food materials conforms to that of the basal diet is an important factor in the determination of infestation.

(ii) The physical condition of food-stuffs may also determine the degree of infestation. The best medium for optimum growth is probably that offered by food grains either in the broken form or in the form of low extraction flour. However, in the case of certain commodities whole grain is also liable to attack by the larva.

(iii) The presence of toxic or repelling substances in the food material is another factor which influences the infestation. Poor development of the larva on some of the pulses and other commodities could have been due to this factor.

(iv) Other factors include food odours and the ability of the food to provide stimuli essential for oviposition. These, however, have not been considered in the present investigation.

SUMMARY

Development of *Corcyra* larvæ on a variety of cereals and millets, pulses, oil-seeds or spices has been studied. Of the various food-stuffs tested, flour of pearl millet and broken grain of wheat proved the best media for the growth of this insect. Results of feeding trials with the various commodities have been discussed in the light of the basal food requirements

* Test with chilli powder was repeated twice.

and the composition of the food offered. The larvæ can flourish in media with a relatively low protein content. On the basis of the results obtained by feeding the larva on fortified media, the factors responsible for a poor development on pulses and other food-stuffs have been outlined. These are the quality of the carbohydrate content and the growth inhibitors. Also the factors which may determine the degree of infestation by *Corcyra, i.e.*, whether this insect can be a major or minor pest of a particular commodity have been enumerated. These factors include physical condition of the food and its chemical composition.

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A BACTERIAL BLIGHT DISEASE OF CORIANDER

By M. C. Srinivasan, M. K. Patel and M. J. Thirumalachar

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Introduction

Coriandrum sativum L. is widely cultivated in India for its aromatic leaves and seeds used as condiment and spice. A severe bacterial leaf-spot and blight was first noticed near Poona, and later in many other places. The damage is often considerable in green plants which are cut and marketed. The diseased leaves under moist enclosed conditions begin to rot and also provide entry for secondary organisms. There is considerable reduction in market value due to rotting of leaves.

Early symptoms of infection are rather inconspicuous and easily escape observation. Infection in the beginning is evident on the leaves in the form of very minute, pale-brown spots surrounded by water-soaked area. The spots later turn dark brown and show the bacterial exudate. Occasionally, the bacterium is found to invade the vein edges and run down the petioles through vascular bundles. Under favourable conditions of infection, whole leaf segments become soft and pulpy.

Isolation and Inoculation Studies

The causal organism was isolated by the dilution poured plate technique using potato dextrose agar medium. Isolations from the young pale-brown lesions as well as from those showing limited vascular infection gave in pure culture a bacterium forming smooth, glistening yellow colonies characteristic of *Xanthomonas* species. Single colonies were sub-cultured on to slants of the same medium, on which a copious, slimy yellow growth was observed after 48–72 hours.

Pure culture of the organism was used to inoculate disease-free plants. Young seedlings as well as coriander plants up to flowering stage were sprayed with the bacterial suspension from 48 hours old culture. The inoculated plants were incubated for 12 hours under moist chamber, after which they were transferred to glass-house for further observations. First symptom of successful infection was noticed on inoculated plants after 10 days, appearing as brown specks on the leaves and vein edges. Re-isolations made from these infection spots yielded a culture identical with the original isolate.

With the pathogenicity of the culture established, further experiments to study the biochemical characters as well as infection behaviour of the pathogen were undertaken. The host range of the bacterium was studied by cross-inoculating hosts closely related to coriander. Ten plants were used in each case. The results of these inoculation experiments are presented in Table I.

TABLE I

Results of cross-inoculation of Xanthomonas *species from coriander on other Umbelliferæ*

Host	Infection behaviour
Coriandrum sativum L. ..	Severe infection
Fæniculum vulgare Gaertn. ..	Severe infection
Daucus carota L. ..	No symptoms
Carum copticum Benth. ..	,,
Cuminum cyminum L. ..	,,
Peucedanum graveolens Benth. ..	,,
Pimpinella sp. (Hort. var.) ..	,,

From these studies it became evident that besides coriander, the natural host, the bacterium is capable of infecting also the fennel (*Fæniculum vulgare*) with equal severity, in artificial inoculation experiments. On the much dissected leaves of the fennel, infection extends as pale water-soaked streaks causing severe blighting of the shoots.

With the other umbelliferous hosts, attention was chiefly focussed on the reaction behaviour of carrot in order to ascertain the relationship of the organism to *Xanthomonas carotæ* (Kendrick) Dowson. Seedlings of the commercial carrot varieties "Goldenheart" and "Oxheart" as well as of four indigenous varieties were inoculated with vigorously growing cultures of the organism. In repeated trials, infection symptoms were observed only on the coriander leaves, while the carrot seedlings remained healthy. This indicated that the organism was different from *Xanthomonas carotæ* which is so far not known in India.

CULTURAL AND PHYSIOLOGICAL CHARACTERS

The bacterium is a short rod with rounded ends, occurring mostly single or in short chains, 1·3–2·0×0·5–0·9 μ, gram negative, capsulated, non-acid fast and motile by polar flagellum. No involution forms have been observed.

The organism makes a profuse growth on various media like potato-dextrose agar, nutrient agar and yeast glucose chalk agar forming smooth bright yellow colonies, with translucent or opaque centres. Slants of these media when inoculated with a loopful of culture get completely covered with copious, butyrous, yellow slime within 72 hours when incubated at 28–30° C. The stock cultures have been satisfactorily maintained for over four years on these media, particularly the yeast glucose chalk medium.

Good growth of the bacterium has been observed on various other synthetic or semi-synthetic media also. Czapek's agar and Patel's sodium taurocholate peptone agar (for selective isolation of *Agrobacterium tumefaciens*) also supported very copious growth of the pathogen.

Nutrient broth was clouded with moderately flaky sediment after 48 hours.

Diastatic activity on starch-agar plates was strong resulting in a digested zone of 25 mm. in 8 days around the colony. Moderate liquefaction of gelatin and digestion of casein were observed in petri plate cultures. Milk was rapidly peptonized and the colour of litmus reduced. Ammonia was liberated when cultured in peptone water. Hydrogen sulphide production was also present in traces in such cultures. Tests for indole production from tryptophan containing medium also gave negative results. Nitrates were not reduced to nitrites in synthetic medium. M.R. and V.P. tests were also negative.

A wide range of carbohydrates were utilised by the organism grown in synthetic medium with the production of acid but no gas. In media containing dextrose, lactose, sucrose, maltose, mannitol, glycerol and dextrin, acid was produced after 5–6 days. Salicin and dulcitol failed to support good growth of the organism.

The bacterium is strictly aerobic and is fairly tolerant to a wide range of pH variations in the medium. A concentration of 2–3% sodium chloride in the medium markedly limited the growth with complete inhibition at 4% concentration. The thermal death-point was $\pm$ 54° C.

PATHOLOGICAL ANATOMY

Microtome sections revealed that the entry of the pathogen is through stomata and infection is confined chiefly to parenchymata. Infection through

the vein-endings causes the bacterium to become vascular and run down the veins for short distances on the leaf surface. Systemic infection has never been observed.

Taxonomy and Nomenclature

The bacterial pathogen under study is closely allied to *Xanthomonas carotæ* (Kendrick) Dowson which has been reported to parasitise only *Daucus carota* L.[1, 2] It, however, differs markedly in its not being pathogenic to carrots as well as in its strong diastatic activity, which character has been reported to be absent from *X. carotæ*.

The bacterium is presented as a new species under the name of *Xanthomonas corianderi* with the following technical description:—

Short rods with rounded ends, $1 \cdot 3–2 \cdot 0 \times 0 \cdot 5–0 \cdot 9 \mu$, gram negative, capsulated, non-acid fast, without endospores, polar-flagellated; butyrous bright yellow colonies with translucent or opaque centres formed on various nutrient media; starch rapidly hydrolysed while gelatin moderately liquefied and casein partially digested; milk peptonized and litmus reduced in litmus milk medium; ammonia and hydrogen sulphide liberated from peptone water; indole not produced and nitrates not reduced; M.R. and V.P. tests negative; acid without gas from various carbohydrates except salicin and dulcitol; aerobic; thermal death-point 54° C.

Hab. : Pathogenic on leaves of *Coriandrum sativum* L. and infecting *Fœniculum vulgare* Gaertn., also in artificial inoculation experiments.

Poona, August–October 1960.

Summary

An undescribed *Xanthomonas* species (*X. corianderi*) inciting leaf-spot and blight of Coriander plant is described. In inoculation studies it was found to infect fennel also (*Fœniculum vulgare*). The species is closely related to but distinct from *X. carotæ* (Kendrick) Dowson.

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ROOT APICAL ORGANIZATION IN MONOCOTYLEDONS—MARANTACEÆ

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Introduction

The authors have reported elsewhere the root apical organization of some members of the families Musaceæ, Cannaceæ and Zingiberaceæ of the order Scitamineæ (Pillai and Pillai, 1961 *a*, *b*; Pillai *et al.*, 1961). This contribution embodies the results of their investigations of the root apices of seven species belonging to four genera of the family Marantaceæ of this order.

Materials and Methods

The techniques described by the authors in their previous reports were followed in investigating the root apices of *Calathea zebrina* Lindl., *Stromanthe sanguinea* Sond., *Phrynium capitatum* Willd., *Maranta variegata* Lodd., *Maranta major*, *Maranta zebrina* Sims. and *Maranta arundinacea* Lindl.

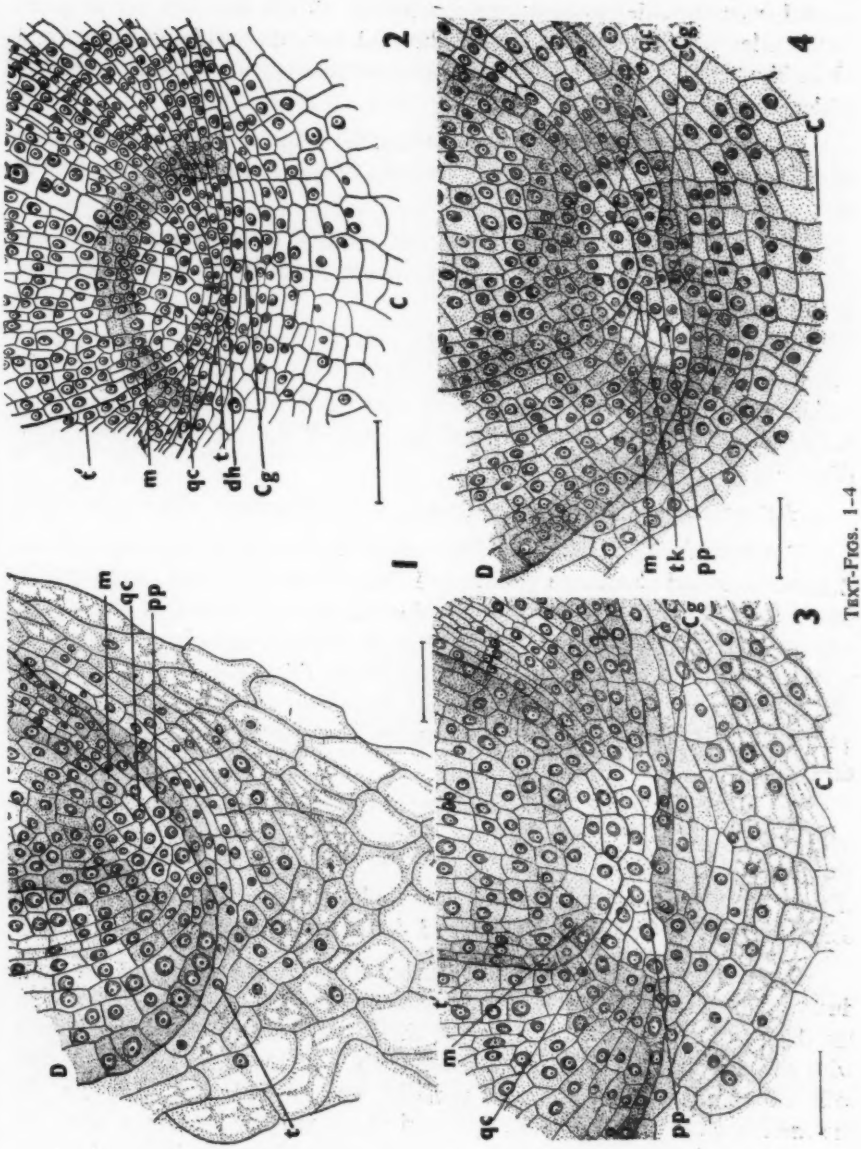
Observations

Structural Organization

This is essentially similar at the root apices of these species, except that in *Maranta arundinacea* which is described separately.

Root-cap.—This is separate from the root body and is composed of two regions, the columella in the middle and the peripheral region around. The central columella does not extend far towards the tip in some roots like those of *Phrynium capitatum* (Text-Fig. 1). Where distinct, it is composed of vertically arranged files of cells. The cells of the meristem, the columellogen, concerned with the production of the columella, divide transversely like a rib meristem (Schopf, 1943; Allen, 1947; Spurr, 1949; Pillai and Pillai, 1961 *b*; Pillai *et al.*, 1961) (Text-Figs. 2–4).

The cells of the peripheral region of the cap can be distinguished from the central columella by the oblique orientation of its cell-rows which are



TEXT-FIGS. 1–4

curved from the sides towards the columella. T-type divisions are frequent at the sides with the head of the 'T' directed towards the flanks as at *t* and *tk* in Text-Figs. 1, 4 and 5. Such divisions enable this region to become wider towards the front.

In transections the cells of the columella appear as a compact mass of polygonal cells in the centre with the cells of the peripheral region around it in radiating rows.

The columella maintains long vertical files of cells. Furthermore, the number of cells across the diameter of the columella is essentially the same at different levels.

When development of the lateral roots is studied, the endodermis is found to give rise to the root-cap and the pericycle to the root body. The middle cells of the endodermis which turn meristematic exhibit periclinal divisions and become distinct from the rest of the meristem very early (Text-Figs. 9–11).

Histogens of the Root Body.—There are two histogens of the root body:

The protoderm-periblem complex.—As in the roots of members of the Zingiberaceæ and Cannaceæ (Pillai and Pillai, 1961 *b*; Pillai *et al.*, 1961), this is located in front of the plerome dome and is composed of one tier of cells in all the species listed here, except in *Maranta arundinacea*, where it is composed of two superimposed tiers of cells (Text-Figs. 2 and 7). The single tier is one to five cells across in the various species. The state of quiescence of the cells in this region makes it slightly difficult to recognize this layer in some cases.

The cells of this tier of initials located on the flanks exhibit T-divisions, with the T-head pointing to the centre, by which the tissue widens out on the flanks. Repetition of such T-divisions results in the formation of a slight concavity at the front of the root body in some cases into which the columellogen fits (*see* Text-Figs. 3 and 4, for instance).

Dermatogen.—This differentiates from the outermost layer of the products of division of the protoderm-periblem complex at some distance on the flanks. Once distinct as a tier, it divides anticlinally and is concerned with the development of the epidermis only. In the quiescent centre the cells are comparatively elongated radially, while a little behind it, *i.e.*, in the meristematic zone, they are thin and short and appear like a stack of coins. Behind this zone the cells again elongate along the long axis.

Periblem.—The cells of this region undergo repeated divisions with the T-head directed to the plerome dome resulting in obliquely oriented

files of cells, *i.e.*, the *Körper* complex (Schüepp, 1917), proceeding from outside the tip of the plerome dome towards the sides. After the periblem has become wide enough the T-divisions give place to anticlinal ones, the cell-rows exhibiting the rib meristem type of activity.

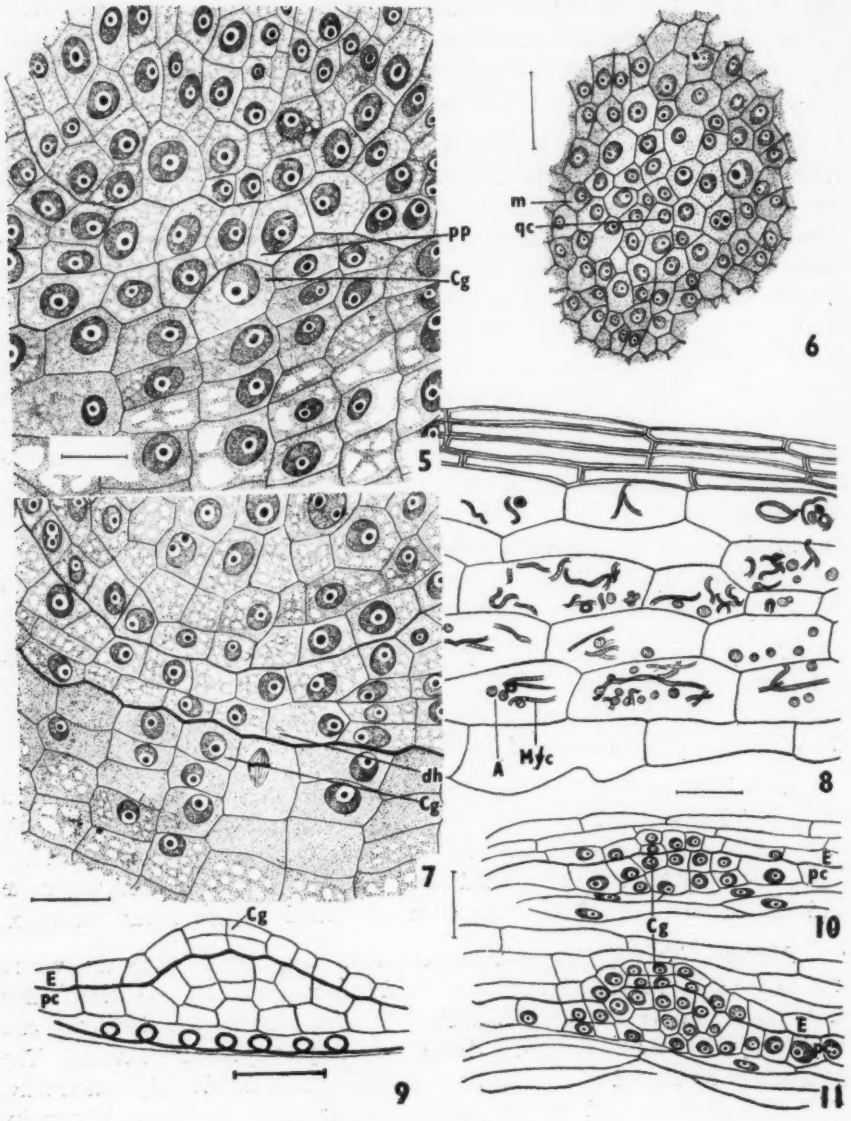
Hypodermis.—This is composed of a few layers of cells. It originates from some of the inner twin daughter cells produced by the T-divisions of the protoderm-periblem complex near the plerome dome before the separation of the dermatogen. These cells undergo further T and periclinal divisions to form the multilayered hypodermis. The cells of the hypodermis become vacuolated earlier than the other cells of the cortex. In *Calathea zebrina* and *Stromanthe sanguinea* these cells develop into a velamen-like tissue (Text-Fig. 8). The cells show a crumpled appearance even near the meristematic zone. These velamen-like cells are mycorrhizal, *i.e.*, they have fungal hyphæ, and algal cells too, inside them. On the inner side of this velamen-like hypodermis there are a few layers of narrow-lumened cells which are much elongated along the long axis of the root. These show thickenings like sclerenchyma in the mature portions of the root. The crumpled cells of the hypodermis, delimited by longitudinal sclerenchymatous cells towards the inside, were found in the roots of *Maranta variegata*, *M. zebrina* and *Phrynium capitatum* also (Plate XIV, Fig. 1).

Cortex has three distinct regions, the hypodermis outside, the longitudinally elongated ring of cells just inside the hypodermis and the rest of the cortex. The cells of the last-mentioned region are polygonal, contain deeply staining cytoplasm and exhibit the rib meristem type of division.

Endodermis.—Near the plerome dome all the cells of the periblem exhibit T-divisions enabling the region to become wide (Text-Figs. 1–3). After a few T-divisions, the innermost of these initials divide only anticlinally. This is the endodermis. The endodermis can, as in members of Zingiberaceæ and Cannaceæ, be said to arise from an endodermis-periblem complex.

Plerome.—This is clearly distinguishable except at the very tip, where due to the cells going to quiescence, the demarcation is not very clear. But close to the dome the outer boundary of this, namely, the pericycle, can be distinguished by its cells with densely staining cytoplasmic contents. The pericycle is composed of a single layer of cells which divide only anticlinally. It is also characterised by the cells retaining their meristematic activity long after the other cells have lost it.

The elements which go to compose the metaxylem vessels can be distinguished very close to the plerome dome by the cells becoming wider and



TEXT-FIGS. 5–11

starting vacuolation early. The cells destined to develop into phloem elements are found, particularly in the transections, by their topography, as

groups of narrow-lumened cells with densely staining cytoplasmic contents and exhibiting longitudinal divisions. From these develop the sieve tubes.

In the centre, the cells exhibit the rib meristem type of division and give rise to the medulla.

The organization of the tip of the roots of *Maranta arundinacea* differs from the others in having a two-tiered protoderm-periblem complex (Text-Figs. 2 and 7). Of these two tiers, the inner is concerned with the formation of the cortex and endodermis while the outer gives rise to only the dermatogen and hypodermis. T-divisions in the outer tier (Text-Figs. 2 and 7) give rise to the initials of the dermatogen and hypodermis. The outer daughter cell of the T may undergo one or two more T-divisions contributing the inner daughter cells to the hypodermis. After this, the outer daughter cell divides only anticlinally and gives rise to the dermatogen. The inner daughter cells undergo further T-divisions forming the multi-layered hypodermis, but they do not contribute cells to the cortex. This can be designated as the "*Dermato-hypodermis complex*".

Thus, the structural organization of the root apices of these species falls under two categories:

(i) with independent plerome and root-cap and a single-tiered protoderm-periblem complex, and

(ii) with independent plerome and root-cap and a two-tiered protoderm-periblem complex.

Cytophysiological Organization

The observations on this aspect correspond to those on members of the other families described already. There is a group of cells characterised by:

(i) lightly stained cytoplasm with pyronin and methyl green and hæmatoxylin (Text-Figs. 2, 4 and 6),

(ii) vacuolation (Text-Figs. 5 and 7),

(iii) smaller nucleoli and nuclei (Table II),

(iv) lesser nucleolus/nucleus ratio (Table II), and

(v) lesser frequency of mitotic figures (Table I).

These features indicate that these cells are in a state of comparative repose. Behind this, as seen in longisections and around it as seen in transections, can be seen cells which have

TABLE I

The number of cells and the number of dividing cells in the quiescent centre and the meristematic zone (as seen in one transection of each root) and the percentage of dividing cells

Species	Quiescent centre			Meristematic zone		
	Total number of cells	No. of dividing cells	Percentage	Total number of cells	No. of dividing cells	Percentage
Maranta arundinacea	93	2	2·15	111	30	27·02
	59	2	3·38	100	25	25·00
	59	3	5·08	102	27	26·42
	50	1	2·00	100	25	25·00
	49	2	4·10	105	29	27·61
Calathea zebrina ..	45	..	0·00	77	15	19·48
	62	2	3·22	117	24	20·51
	62	2	3·22	104	14	13·46
	48	1	2·10	76	15	19·50
	61	2	3·27	100	15	15·00

TABLE II

Areas of cell, nucleus and nucleolus in the quiescent centre and meristematic zone in sq.μ (mean of 20 determinations) and the respective nucleolus/nucleus and nucleus/cell ratios

Species	Cell	Nucleus	Nucleolus	Nucleolus / Nucleus %	Nucleus / Cell %
		Quiescent Centre			
Maranta arundinacea ..	53·84± 34·00	13·23 ± 3·20	0·6000± 0·1154	4·52	24·62
Calathea zebrina ..	51·61± 16·22	13·308± 4·042	0·6669± 0·2107	5·01	25·78
		Meristematic Zone			
Maranta arundinacea ..	84·30± 25·69	17·57 ± 3·74	2·4053± 0·0385	13·68	20·84
Calathea zebrina ..	55·50± 16·09	13·815± 3·831	1·5507± 0·4034	11·22	24·80

(i) densely staining cytoplasm,

(ii) vacuolation not prominent,

(iii) larger nucleoli and nuclei (Table II),

(iv) greater nucleolus/nucleus ratio (Table II), and

(v) greater frequency of mitotic figures (Table I).

These features indicate that these cells are in a state of activity. The former region is called the quiescent centre (Clowes, 1956, 1958), while the region around it is called the meristematic zone (Pillai and Pillai, 1961 *a*, *b*). This meristematic zone is in the form of a ring recalling the *anneau initial* of Plantefol (1947) (Text-Fig. 6).

Discussion

Structural Organization

The older literature mentions the type of structural organization met with in the first six species with independent initials for the plerome and root-cap outside and a single-tiered common initial zone for the protoderm and periblem, the protoderm-periblem complex, as occurring in grasses whereas it is found in members of Zingiberaceæ, Cannaceæ (Pillai and Pillai, 1961 *b*; Pillai *et al.*, 1961) and in those of Xyridaceæ (Unpublished). Haberlandt (1914) and Hayward (1938) also mention this as their type 2 and as being common to Gramineæ, Cyperaceæ and Juncaceæ. Esau (1953) does not mention such a type of organization at all as being present among Monocotyledons. Popham (1952), on the other hand, mentions this as the principal monocotyledonous type, though the examples that he cites are mainly from among the grasses. Pillai and Sachdeva (1960) have reported it in *Sorghum vulgare*. It appears that it is an important type of structural organization among Monocotyledons.

Root-cap formation.—The root-cap is independent as in Zingiberaceæ and Cannaceæ (Pillai and Pillai, 1961 *b*; Pillai *et al.*, 1961). The calyptra is assumed to be a proliferation of the dermatogen (Hanstein, 1868; Haberlandt, 1914) without any separate histogen being concerned with its formation. Holle (1876) also does not consider it as originating from a separate meristem.

As pointed out by the authors before in the members of the Zingiberaceæ and Cannaceæ (Pillai and Pillai, 1961 *b*; Pillai *et al.*, 1961), the calyptra is distinguishable into two distinct regions on the basis of types of cell complexes. In the middle is the columella, where the cells are arranged in superimposed tiers forming vertical files. This is produced by a meristem

which exhibits mainly transverse divisions. The rest of the cap is composed of obliquely arranged files of cells curving from the flanks towards the columella and form the "*Kappe*" complex of Schüepp (1917). This region is produced by a meristem whose cells exhibit the T-type of division with the head of the T pointing towards the flanks. The expression 'peripheral region', as used by Allen (1947) and adopted by the authors before, is used here also for this meristem and the term 'columellogen' which the authors (1961 *b*) introduced is continued to be applied to the former. While studying the lateral root development in *Canna indica*, *Maranta variegata* and *M. zebrina*, it has been found that the columellogen becomes distinct from the rest of the meristem very early in the formation of the lateral root (Text-Figs. 9–11).

Histogens of the Root Body: There are two types of configuration met with at the root apices of these plants:

(1) Where there is an independent, single tier of cells which is the common initiating zone for the epidermis and cortex. This is met with at the root apices of *Phrynium capitatum*, *Calathea zebrina*, *Stromanthe sanguinea*, *Maranta variegata*, *M. major* and *M. zebrina*. This common tier has been termed by van Tieghem and Douliot (1888) as the 'epistele', Schade and Guttenberg (1951) and Clowes (1954) as the 'Periblem-Dermatogen Complex' and by Kasapligil (1954) as the 'Protoderm-Periblem Complex'. The term protoderm, according to Haberlandt (1914), comprehends something more than the dermatogen as it may give rise to the subepidermal layers also. Since in these roots a common tier gives rise to the dermatogen and subepidermal layers also, the authors prefer the term protoderm in the expression 'Protoderm-Periblem Complex', as they did before (Pillai and Pillai, 1961 *b*; Pillai *et al.*, 1961).

(2) Where there is an independent plerome and two tiers of cells which form the initiating zone for the dermatogen and periblem. This is a modification of the previous type and is met with in *Maranta arundinacea* only of all the species investigated by the authors. In this the outer tier gives rise to the dermatogen and hypodermis while the inner one is concerned with the production of the rest of the cortex. Such an organization has not been mentioned by any investigator till now. The outer tier of the two-tiered protoderm-periblem complex undergoes the T-type of division near the proximal end just outside the plerome dome (Text-Figs. 2 and 7). The inner twin daughter cell of this division is concerned with the formation of the hypodermis only, its further proliferation not contributing to the cortex. The outer daughter cell may undergo a few more T-divisions, the

inner daughter cells of which are contributed to the hypodermis. Ultimately, the outer daughter cell divides anticlinally only and gives rise to the epidermis. Such a zone of initials is being reported for the first time and has been named the "*Dermato-Hypodermis Complex*".

Dermatogen.—This expression is used by the authors in a restricted sense only, as was before, because the initial does not form a distinct tier as first enunciated by Hanstein (1868), but differentiates from the protoderm-periblem complex or the dermato-hypodermis complex as the case may be. Esau (1953) states that in roots the "dermatogen is supposed to be the outermost layer of the cortex". In these species, this layer does not arise as an independent tier and can be considered as the outermost layer of the cortex to some extent.

Periblem.—These initials exhibit T-divisions with the head of the T pointing towards the plerome dome and producing oblique files of cells of the '*Körper*' type (*Schüepp*, 1917), curving outwards from the plerome dome and running in a direction opposite to the oblique files of the '*Kappe*' type in the peripheral region of the cap. The periblem is usually composed of the cell layers extending from just outside the pericycle, all these originating from the tier of initials located outside the plerome dome. The exception to this is *Maranta arundinacea* where the hypodermis and dermatogen arise from one tier of initials and the rest of the cortex from another tier.

Hypodermis or Exodermis (?).—There is considerable confusion in the use of these two expressions in the literature. Both the terms have been used in fundamentally different senses and many a time synonymously. It is, therefore, necessary to clarify this.

In the older literature (Jörgensen, 1878; Sachs, 1882; Sielder, 1892) the hypodermis refers to the outermost cortical layer next to the epidermis. Solereder and Meyer (1929), Guttenberg (1943), Krauss (1949) and Foster (1949) consider this layer just inside the epidermis as the exodermis. This term is used by Esau (1953) also in the same sense whereas Eames and MacDaniels (1947) call it the hypodermis. Van Fleet (1950) refers to the hypodermis as a mirror-image of the endodermis whereas Mulay and others (Mulay and Panikkar, 1956; Mulay and Deshpande, 1959) consider that the exodermis is a tier of cells found only in those roots where velamen develops and where it is a mirror-image of the endodermis. Thus, there is no consensus of opinion regarding the use of these terms. The authors do not find any layer which is the mirror-image of the endodermis. The term hypodermis is preferred by the authors following Mulay and others to designate the multi-layered tissue found topographically just inside the epidermis

and differentiated in some morphological characters from the cortical cells on the inside. In the first six species described here, this tissue arises ontogenetically from the same initials as for the periblem.

In *Maranta arundinacea* the ontogeny of the hypodermis is slightly different. Whereas in the other species there is a single-tiered protoderm-periblem complex from which the dermatogen and hypodermis arise, in *M. arundinacea* there is a two-tiered protoderm-periblem complex. The outer tier is giving rise to the dermatogen and hypodermis only (Text-Fig. 2). Thus, these two tiers are themselves separable.

In the roots of *Maranta variegata*, *M. zebrina*, *M. major*, *Calathea zebrina*, *Stromanthe sanguinea* and *Phrynium capitatum*, the hypodermal cells are separated from the inner region by two to four layers of long, narrow-lumened and uniformly thick-walled cells (Plate XIV, Fig. 1). These cells do not show any thickenings on the outer walls nor the long and short cells characteristic of the exodermis (*see* Mulay and others, *loc. cit.*). The hypodermal cells in these species have algal cells and mycorrhizal hyphæ in them (Text-Fig. 8). The criss-cross thickenings of the walls characteristic of the velamen are not present. Though it cannot be called velamen, it may be something akin to velamen or an incipient velamen.

Endodermis arises, as in the roots of members of Zingiberaceæ and Cannaceæ reported earlier (Pillai and Pillai, 1961 *b*; Pillai *et al.*, 1961) from the innermost layer of periblematic cells, *i.e.*, from an endodermis-periblem complex.

Plerome.—Initials for this are independent and normal in their activity giving rise to the pericycle, vascular elements and pith.

Cytophysiological Organization

At the tips of these roots also could be distinguished a group of cells constituting a quiescent centre surrounded on the side of the root proper as seen in longisections and around it as seen in transections, by cells in a more active state, named by the authors as the meristematic zone (Text-Fig. 6). The latter region appears to be the actual site of meristematic activity as was shown by some surgical experiments (Pillai and Sachdeva, 1960; Pillai and Pillai, 1961 *c*). The similarity between these regions and the postulates of *anneau initial* by Plantefol (1947) and *meristeme d'attente* by Buvat (1952) has been pointed out before.

SUMMARY AND CONCLUSIONS

The root apices of seven species included in four genera of the Marantaceæ exhibit two types of structural organization. Six of them have

independent initials for the plerome inside and the root-cap outside and a single tier of cells, the protoderm-periblem complex, from which arise the dermatogen and periblem. The seventh species shows independent initials for the plerome and root-cap and a two-tiered protoderm-periblem complex, of which the outer tier gives rise to the dermatogen and hypodermis only, named the "dermato-hypodermis complex" and the inner to the rest of the cortex.

The cap is divided into two regions on the basis of the cell complexes present, the columella in the middle and the rest of the cap. The meristems concerned with the formation of these two regions are found to be separate, the one forming the columella being called the columellogen and the other, the peripheral region.

These roots show a division of the cortex into a hypodermis separated from the parenchymatous cells on the inside by a few layers of sclerenchymatous narrow-lumened cells in the middle.

The hypodermal cells show the presence of mycorrhiza and algal cells. The probable relation of this with the velamen tissue is discussed.

The endodermis is traced to an initiating zone common with the periblem, named as the endodermis-periblem complex.

The cytophysiological state of the cells is very important from the histogenetic point of view. These roots also exhibit a quiescent centre, around and behind which the actively dividing cells constituting the meristematic zone could be distinguished. The characteristics of the cells composing these two zones are described. It is further emphasized that this aspect also be considered in root apical studies to have a more lucid picture of the apical organization.

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Addendum

Guttenberg (Linsbauer's *Handbuch der Pflanzenanatomie*, Bd. 8, *Teil* 3, 1960) has put forward some ideas in a recent publication, which appeared after these reports were sent to the press, which deserve mention.

He divides root apices into two types. The first is the "*open*" type where there is a common generative centre for all the histogens. The second is the "*closed*" type with discrete initials. The root apical structures of most of the members reported here fall under the second type and only that of *Zingiber officinale* falls under the first type.

Guttenberg also mentions that a closed type of organization met with in the early embryo stages may change to a partially or fully open type as the embryo grows older and the root grows for about 6 to 8 days after the seed germinates. In the present investigations it has not been possible to study the embryo stages and the development of the apical structures as the root grows out at seed germination because in many cases the habit of seed setting has been lost and the plants propagate vegetatively. So, the development of the lateral root was studied where such a transition is not found and the structural configuration at the tips of the lateral and main roots is similar.

Guttenberg calls the 'dermatogen' which arises from the products of division of the dermo-periblem complex (as obtaining in these cases) the "*secondary dermatogen*", which appears to be more apt.

The development of the columella has been described by Guttenberg from the embryo onwards. He has also described the initials for the columella as independent even from the early embryo stages, as the authors have tried to bring out here. But, the oblique divisions of the periblem initials located on the flanks which are described by Guttenberg as the contribution of the periblem to the initials of the secondary columella, are not observed in these root apices. The knee formation connecting the columella flanks and periblem is not noticeable in these materials. Instead, the two types of cell complexes, namely, the *kappe* type characteristic of the peripheral region and the vertical files of the columella, are clearly distinguishable in these.

The quiescent centre concept does not find favour with Guttenberg, who states that there are no quiescent cells and that the cells at the root tip are dividing. But, the development of a quiescent centre has been found by Jensen (*Proc. nat. Acad. Sci., Wash.*, **44,** 1038–46, 1957; *Exp. Cell. Res.*, **14,** 575–83, 1958) and more recently by Davidson (*Ann. Bot., N.S., Lond.*, **24,** 287–95, 1960), experimenting with radio-isotopes. The present reports and those being reported by the authors elsewhere, do not deny the presence of some divisions in the cells at the tip of the root body; however, these cells are not normal in their activity as far as the regeneration of the root apex

is concerned as shown by their reaction to some surgical experiments (Pillai and Sachdeva, *Curr. Sci.*, 1960, **29**, 232–34; Pillai and Pillai, 1961 *c*).

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* Originals not seen.

EXPLANATION OF TEXT-FIGURES

TEXT-FIGS. 1–4. Fig. 1. *Phrynium capitatum.* Median L.S. of root apex with discrete plerome and root-cap and a single-tiered protoderm-periblem complex. The quiescent centre to the root body lined by the cells of the meristematic zone in the form of an arch can also be seen. Fig. 2. *Maranta arundinacea.* Median L.S. through the root apex showing independent plerome and root-cap and a two-tiered protoderm-periblem complex, of which the outer is the dermato-hypodermis complex. The stippled region shows the boundary between the quiescent centre and the meristematic zone. Fig. 3. *Calathea zebrina.* Median L.S. through the root apex showing the independent plerome and root cap and single-tiered protoderm-periblem complex and the quiescent centre and the meristematic zone behind it in the form of an arch. Fig. 4. *Stromanthe sanguinea.* Median L.S. of root apex having discrete plerome and root-cap and a single tier of protoderm-periblem complex. The quiescent centre to the root body lined in the form of an arch behind the meristematic zone can be made out.

C–Columella; Cg–Columellogen; D–Dermatogen; dh–Dermato-hypodermis complex; m–Meristematic zone; pp–Protoderm-periblem complex; qc–Quiescent centre; t–T-divisions

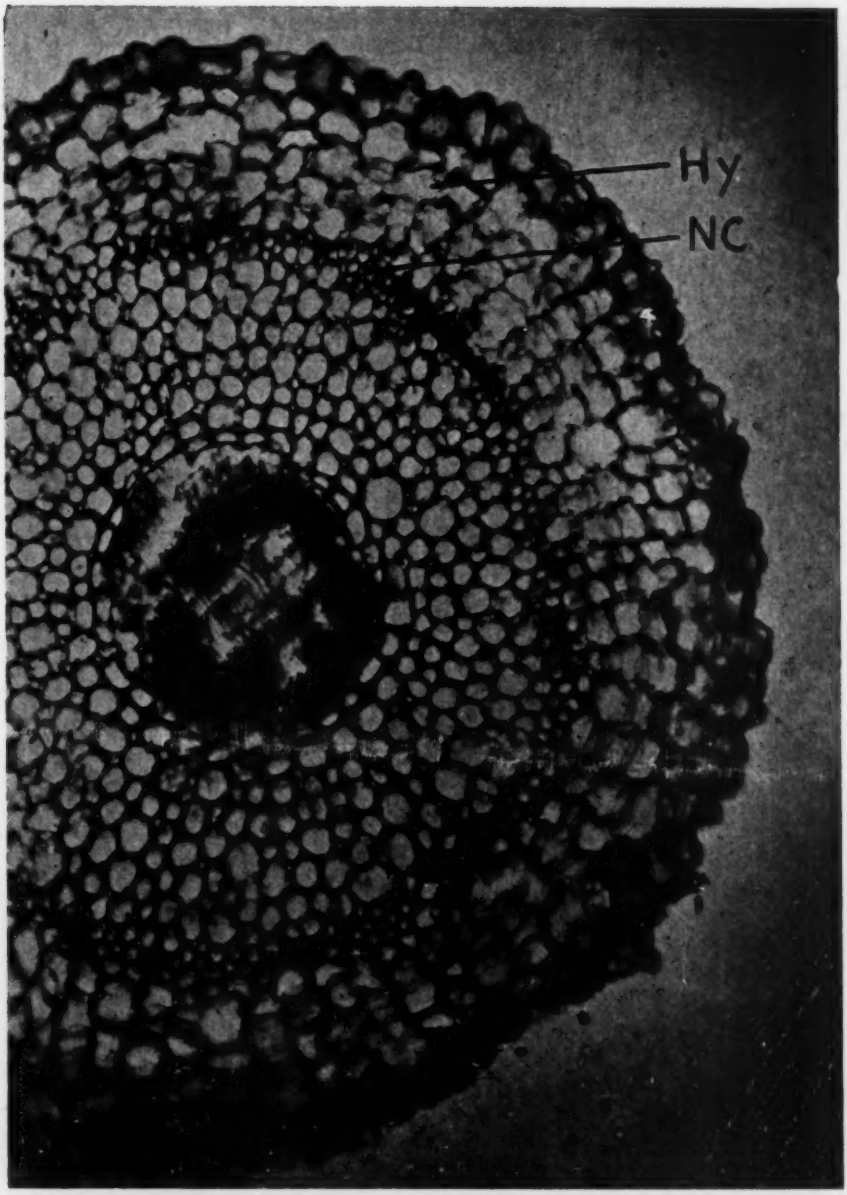

FIG. 1. *Phrynium capitatum.* T.S. of root with the three zones of the cortex, the velamen-like hypodermis of crumpled cells outside (Hy), the narrow-lumened, thick-walled cells (NC) and the parenchymatous cells inside (× 180).

of the peripheral region; t'-T-divisions of the endodermis-periblem complex; tk-T-divisions of the *Kappe* and *Körper* types. (All scales = 50 μ).

TEXT-FIGS. 5–11. Fig. 5. *Maranta variegata*. Portion of the root apex magnified to bring out the cytophysiological state of the cells of the root body and root-cap. Fig. 6. *Phrynium capitatum*. T.S. of root apex. The quiescent centre is surrounded by the meristematic zone. Fig. 7. *Maranta arundinacea*. Portion of root apex enlarged to bring out the cytophysiological state of the cells of the root body and root-cap. Fig. 8. *Calathea zebrina*. L.S. passing through the outer part of the cortex showing the velamen-like cells of the hypodermis having mycorrhiza and algal cells, lined on the inner side by thick-walled, small-lumened cells. Fig. 9. *Maranta zebrina*. L.S. through the developing lateral root. The endodermis is giving rise to the cap in which the middle rows show periclinal divisions to give rise to the columellogen, the pericycle, giving rise to the root body. Figs. 10 and 11. *Maranta variegata*. L.S. passing through developing lateral roots showing the endodermis giving rise to the root-cap and the pericycle to the root body. Note the periclinal divisions of the middle cells of the endodermis to give rise to the columellogen.

A–Algal cells; Cg–Columellogen; dh–Dermato-hypodermis complex; E–endodermis; m–Meristematic zone; Myc–Mycorrhiza; pc–Pericycle; pp–Protoderm-periblem complex; qc–Quiescent centre. (Scales in Text-Figs. 5, 7 and 9 = 20 μ, and in Text-Figs. 6, 8, 10 and 11 = 50 μ).

ROOT KNOT OF *GOMPHRENA GLOBOSA**

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(Communicated by Dr. S. N. Das Gupta, F.A.SC.)

Introduction

Root knot of *Gomphrena globosa* was observed during the study of the leaf blight disease of *Gomphrena* caused by *Alternaria gomphrenæ*. The affected plants were stunted, the foliage showed withering with extreme discolouration and yellowing and the root system exhibited marked hypertrophy and abundant formation of galls on the main as well as lateral roots and root hairs presenting a typical bead-like appearance. The gall size on the roots varied from less than 0·5 mm. in diameter in root hairs to larger dimensions in the main roots. At the advanced stage of the disease plants wilted, roots showed club foot formation and were finally found to rot giving out an unpleasant odour.

The examination of the different parts of the hypertrophied roots and galls showed the presence of a species of *Fusarium* together with eggs and adult stages of a nematode later identified as *Diploscapter coronata* Cobb. all over the parenchymatous tissues. *Fusarium* is a well-known root-infecting pathogen and nematodes are known to produce galls in infected tissues. Goodey reports the nematode *Heterodora marioni* to be parasitic on *Gomphrena globosa* and *D. coronata* as only a saprophagous species on the same plant. The present paper is an attempt to show the parasitic nature of *Diploscapter coronata*. The main findings of the author as given in a personal communication has been quoted by Chauhan (1957).

Isolation and Identification of the Nematode

The nematodes infecting the roots were cultured in nutritive medium. For this purpose the diseased roots were repeatedly washed with sterile distilled water and the inner tissue of the galls containing the adults and the eggs of the nematode was transferred to the culture tubes by means of a sterile needle.

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* The work was completed in 1948 but for unavoidable reasons could not be published earlier.

‡ Maiden name.

Pure culture of the nematode with nemerous eggs were obtained by careful transfers through several successive generations.

Cultures containing the female larvæ and the adult females of the nematode fixed in 70% alcohol were sent to Dr. B. S. Chauhan, Zoological Survey of India, for identification. Through his kind help and courtesy the nematode was identified as *Diploscapter coronata* which was further confirmed by Prof. Goodey, Rothamstead Experimental Station, England.

Experimental

Materials

Host.—The two varieties of *G. globosa*, Lucknow white and Lucknow purple were utilised for the study.

Parasite.—Pure growths of the *Diploscapter* isolated from galls of *G. globosa* freed from all contaminations were kept as stock culture. These were sub-cultured periodically and utilised for infection experiments. In order to make nematode suspension, contents from these tubes having male and female adults and numerous eggs to different stages of hatching out were mixed with sterile distilled water soon before the experiments and were kept ready for use.

Soil.—Ordinary garden soils in pots with adequate amount of organic matter properly sterilised by autoclaving were utilised for growing *Gomphrena* plants.

Methods

The experimental plants raised from surface sterilised seeds of Lucknow white and Lucknow purple were grown in sterilised soil and when seedlings have emerged healthy ones from these were transplanted in proper pots in predetermined numbers.

Three different ages of plants were used for inoculation experiment: (1) 1½″ seedlings with one pair of cotyledons, (2) 3″ seedlings with five to seven leaves, and (3) mature plants (8–10″).

Inoculation experiments were done by pouring thick nematode suspension at the bases of plants in order that the nematodes can reach the rhizosphere region easily.

Results

100 seedlings each of the first two stages of growth were inoculated by nematode suspension and 50 of each was kept as control which did not receive the parasite. Any indication of the deviation from the normal growth was

noted periodically and representatives of diseased plants were fixed in alcohol (75%) for the study of the histopathology and a few were used for the re-isolation of the parasite from the diseased tissue.

Young seedlings when infected were found to die quickly before galls were produced. Both Lucknow purple and Lucknow white behaved similarly in this respect. The reisolations from the roots of such seedlings soon after their death did not show the presence of *Fusarium*. The presence of nematode was detected both by culture and histopathological studies.

For infection experiment with mature plants, 138 plants of Lucknow purple and 135 plants of Lucknow white were sown in May and when these had attained maturity (8–10″) nematode suspension were poured in the soil as described before and the plants were kept under periodic observation. About 35 plants of purple and 45 plants of the white variety died due to heat leaving 103 of Lucknow purple and 90 Lucknow white for the study of the development of the disease. At the end of October all the plants were up-rooted and examined for galls and nematodes in the root system. The results are given in Table I. No disease was observed in the controls, but a number suffered mortality due to heat.

TABLE I

Experimental infection of mature plants of Gomphrena globosa *by* Diploscapter coronata

Variety	No. of plants	Early symptoms	Advanced symptoms	Healthy	Percentage of infection
Lucknow purple ..	103	0	92	11	90
Lucknow white ..	90	37	0	53	27·3

It is seen that the infection is more severe in purple variety than in the white which is more resistant. In the latter the disease did not progress beyond the early stages. The earlier symptoms as indicated by the etiolation of leaves and visible whitish galls in roots appeared in August and the disease reached its climax in October, when majority of affected plants showed advanced stages of infection. A number of galls randomly selected and carefully teased out were found to contain eggs in various stages of formation.

Histopathology

The histopathology of the diseased roots were worked out using the representatives of experimentally infected seedlings and mature plants. Both hand and microtome sections were prepared which were usually stained with cotton blue or acid fuchsin in lactophenol.

Seedlings.—Duly stained longitudinal and transverse microtome sections of the hypertrophied roots of 2-3 weeks old infected seedlings with single pair of cotyledonary leaves showed the invaders in the ground tissue of the root, surrounding the stellar region. The cells of the parenchymatous tissue which displayed hypertrophy were void of protoplasm and cell contents; instead the nematode filled the cells (being either coiled or fully stretched) bringing about increase in cell dimension, thus resulting in hypertrophy.

Mature Plants.—In mature plants where the club foot appearance was pronounced, despite excessive malformation, it was the cortical tissue and not the stellar region which was the lodging zone of the adult worms, and also of the egg cysts. *Diploscapter coronata* like other parasitic forms was found to live in the ground tissue of the roots and did not invade the stele.

Galls.—The histological study of the galls as they appeared on the pin spots to whitish bead-like structures showed that the natural tissues round the cysts were greatly hypertrophied forming compact 3-4 layers. The presence of these in large numbers resulted in the distortion of the stellar region. At a later stage with the increase in the activity of the cysts the outer cortical tissue gradually disintegrated.

Discussion

Many crops and ornamental plants are known to be attacked by plant parasitic nematodes. Some of these are specialised, others are polyphagous. The symptoms produced by nematode disease are complicate by the symptoms due to the presence of secondary invaders, especially when it is another disease-producing organism like *Fusarium*.

There are several types of nematode disease, *viz.*, root knot produced by *Meloidogyne* (*Heterodora marioni*); root lesion caused by *Pratylenchus* known also as meadow nematodes, in which nematodes feed on cortex of roots destroying the cells; stubby root nematodes (species of *Trichodorus*) and sting nematodes (*Belonolaimus gracilis*) both external parasites which eat up the root-tips so that root systems cannot develop and the shoots become stunted; stem and bulb nematode (species of *Ditylenchus*) responsible for localised deformation of stems and leaves and soft rot of bulbs of Narcissus, Onion, etc.; and wheat nematode (*Aguina tritici*) which invade developing

ears transforming the grains into galls looking much like smut balls (Taylor 1953).

Root knot is known to occur in stone fruit trees (Fikry, 1939), pineapple (Godfrey and Oliveira, 1932), cereals like rice (Atanasoff, 1925; Tullis, 1934; and Steiner, 1934), potatoes, sweet-potatoes (Eliott, 1918; Poole and Schmidt, 1934), yams (Steiner and Buhrer, 1934) and a wide range of other host plants, such as alfalfa, beans, celery, cotton, cowpeas, peanuts, peppers, soya-beans, sugar beet, tomato and tobacco, etc. Godfrey *et al.* (1934) have worked on the trap crops of nematodes and their use in reducing nematode infestation.

During recent years the study of nematode diseases of plants has made a rapid progress and there is an extensive bibliography on the subject including several books (Goodey, 1933, 1951; Filipjev *et al.*, 1941) and reviews (Chitwood and Oteifa, 1952; Fielding, 1959). Hence no attempt has been made here to give a complete bibliography.

Goodey (1933) reports a nematode *Heterodora marioni* as a parasite in *Gomphrena globosa* causing root knot and regards the species of *Diploscapter coronata* as saprophagous. In the root knot of *Gomphrena* under investigation the nematode *Diploscapter* was found associated with a species of *Fusarium* which later on proved to be wilt producing. When separated from this *Fusarium* the nematode was found capable of infecting both the seedlings and mature plants of *G. globosa*. But while the infected seedlings were killed before the formation of galls, typical root knots were produced in the infected mature plants. The experiments have also revealed the existence of varietal difference in the reaction of the host tissue to the invading nematode. In the Lucknow white variety all the infected plants showed advanced symptoms of root knot at the final stage of the disease whereas in Lucknow purple symptoms never proceeded beyond the early stages. The experimental evidence clearly pointed out that *Diploscapter coronata* can act as a parasite on *Gomphrena globosa* in a way similar to *Heterodora marioni*.

SUMMARY

A root knot disease of *Gomphrena globosa* has been described. The disease exhibits typical symptoms, hypertrophy, formation of galls and club foot appearance of root system and stunted growth of shoot.

Histopathology of the diseased roots was studied which showed the presence of the nematode in various stages of egg formation and the presence of adult in the extra-stellar region.

The disease was experimentally produced in two varieties of *Gomphrena globosa*, Lucknow white and Lucknow purple by growing these in nematode-infested soil. Young seedlings quickly die before formation of galls; the more mature plants produce typical galls and finally die.

There is a varietal difference in the reaction of the root tissue of the host to the invading nematode.

The causal nematode has been identified as *Diploscapter coronata* which is generally regarded as saprophagous.

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